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Edited by
GORDON GUNTER
INSTITUTE OF MARINE SCIENCE
THE UNIVERSITY OF TEXAS
PORT ARANSAS, TEXAS

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The External Morphology of *Blias prionoti* Krøyer, a Copepod Parasite of the Sea Robins *(Prionotus)*

By

David Causey

University of Arkansas

SYNONOMY

1863 *Blias prionoti* Krøyer, Naturh. Tidsskrift., ser. 3, vol. 2, p. 262, pl. 12, fig. 5.

1932 *Blias prionoti* Krøyer, Wilson, C. B., Bull. U. S. Nat. Mus., No. 158, pp. 493–494, fig. 296a.

1947 *Blias prionoti* Krøyer, Pearse, A. S., J. Elisha Mitch. Sci. Soc., vol. 63, p. 14.

1952 *Tuccopsis pinguis* Pearse, A. S., Pub. Inst. Mar. Sci., vol. 2, pp. 13–15, figs. 28–37.

1952 *?Tucca sp.* Pearse, A. S., *ibid.*, pp. 12–13, figs. 23–27.

INTRODUCTION

The genus *Blias,* with the monotypic species *prionoti,* was established by Krøyer in 1863, being based upon a single specimen from the gills of a sea robin *(Prionotus)* taken from the Brazilian Coast. Wilson (1932) reported a second collection of two females, also from the sea robin, which had been collected at Woods Hole, Massachusetts, in 1904. Contrary to his usual custom, Wilson did not redescribe this apparently rare and inadequately known species. He copied one of Krøyer's figures, omitting the second of the pygmy males in Krøyer's illustration. Wilson's record, as he stated, is the first for North America. Later Pearse (1947) recorded two females and a male "that apparently belonged to this species" from Beaufort, N.C.

The fourth record of the species and the first from the Gulf of Mexico is, in my opinion, Pearse's (1952) report of *Tuccopsis pinguis, gen. et. sp. n.*, also from the sea robin *(Prionotus pectoralis* and *P. martis)*. This description was based upon seven specimens from the gills of the host. Through the courtesy of Dr. Fenner A. Chace, Jr. and the U.S. National Museum I have been able to examine a slide containing five of Dr. Pearse's type collection of *Tuccopsis.*

This paper is the fifth report on the species and the second report from the Gulf of Mexico. It is based upon 22 collections of 62 females, most of which have associated pygmy males, made at Pascagoula, Mississippi in the summer of 1953. An additional supply of the copepod left on the hosts was not used in this report. Three species of *Prionotus* were present at Pascagoula. *P. rubio* was the most common, *P. pectoralis* was less common, and *P. scitulus* the least common as we encountered the fish. *Blias* is found on all of these species, but most of the specimens came from *P. rubio.* All my specimens came from iced fish passing along the conveyor belts of the Coast Fisheries Division of the Quaker Oats Co. I am indebted to the plant manager, Mr. R. Leonard Davis, and to his staff, for many courtesies which made our collecting a success. As always, I am also indebted to my wife, Dr. Nell B. Causey, for most of the collections, for the identification of the fish hosts, and for calling my attention to the fact that our *Prionotus* had two different copepod parasites. What she saw with the unaided eye I could verify only with the dissecting microscope. Dr. Pearse's *Brachiella rotunda,* a very attractive little fellow, occurs in the mouth and *Blias prionoti* on the gills. We found no exception to this distribution. For the present study 15 whole mounts of the females have been prepared, two being teased preparations. Suitable whole mounts and alcoholic specimens, No. 96038, are deposited in the U.S. National Museum.

MORPHOLOGY

The specimens taken from the chilled and dead sea robins are well preserved but most unfortunately, pretty well covered with a congealed mucus to which debris sticks. The mucus makes cleaning up the parasite generally difficult and almost impossible in the important area of the mouth parts. Much can be picked off with insect pins inserted in match sticks while working under the wide field dissecting binocular but I have not got a single specimen entirely free from such material. Most of my specimens are mounted in the General Biological Supply House's non-resinous mounting medium which gives superb temporary preparations but which practically always go bad within a few months.

Figures 1 and 2 are, respectively, a lateral and a dorsal view of the female copepod and the attached male as removed from a gill filament and preserved in alcohol. The bulbular swellings of the head and of the body may be somewhat overemphasized by the shading, but a good general idea of the female and her attached egg strings, and also of the relative size of the female and the attached pygmy male is obtained. One of the latter is almost always attached to the female in the area indicated, and not uncommonly one or more will be found attached elsewhere, especially near a thoracic appendage, as figured by Krøyer. Specimens processed to mount in balsam shrink and become somewhat wrinkled, while those mounted in the non-resinous mounting medium shrink slightly and at the same time become somewhat distended so that the bulbous processes are no longer evident. I have seen nothing within the specimens except bands of striated muscle fibers, and suspect that by the time the eggs have been extruded they are little more than empty sacs. Measurements for 5 female specimens in alcohol are: total length (exclusive of holdfast organs) from 2.0 mm. to 2.6 mm., with the average being 2.3 mm.; length of body (total length minus head length), 1.3 mm. to 1.8 mm., the average being 1.7 mm.; greatest width of body, usually in region of thoracic appendages, 1.0 mm. to 1.5 mm., the average being 1.2 mm. In the non-resinous mounting medium the dimensions for 10 specimens are: total length, 1.6 mm. to 2.8 mm., with the average being 2.0 mm.; length of body, 1.1 mm. to 2.1 mm., with the average being 1.5 mm.; greatest width of body, 0.7 mm. to 1.4 mm., with an average of 1.0 mm. The egg strings are not included in the total lengths, being highly variable and usually 2 to 3 times the length of the body. These approximate the comparable measurements given by Dr. Pearse. The total length of the pygmy males, as measured in the non-resinous mounting medium, ranges from 0.35 mm. to 0.5 mm., with an average for 5 being 0.4 mm. These figures are not comparable with the figures given by Pearse *(cf. infra)*.

At the apex of the head is a pair of chitinous holdfast organs (fig. 4), which apparently have been overlooked by previous investigators, except possibly Pearse *(cf. infra)*. Each branches distally into 2 or 3 prongs, and *in situ* these are embedded in the gill filament tissue. Each holdfast organ is surrounded by a structureless layer which appears to be a secretion by the gill in response to the presence of the holdfast organ. Krøyer figured and Wilson copied "first antennae with few segments." I am unable to satisfy myself that they are present. The area around the holdfast structures is usually more or less obscured by mucus and detritus. The holdfast organs are sometimes pulled out when the parasite is removed from the gill (which must be the reason why such conspicuous structures have been overlooked) and when that occurs one or more bands of striated muscle fibers are left protruding from the torn area of the head. I suspect, on the basis of my present knowledge, that these bits of muscle bands have been interpreted as antennae. The location would suggest that the holdfast structures are derived by modification of antennae, but whether or not this is true, and if so, from which pair, can be established only when developmental stages are available. I have not found any.

The mouth parts occur in a weakly chitinized and somewhat triangular area on the ventral side of the head. The distal portions of the mouth parts are well chitinized and I feel that such details (fig. 3) are reasonably accurate in my figure, but the proximal portions blend so imperceptably with the body surface, especially in the case of the mandibles, that I despair of ever being certain. The mandibles include a pair of crescentic structures, each of which bears teeth whose ridges extend transversely to the length so as to look somewhat like a coarse file. Pearse (1952) says there are about 14 of these and my counts are approximately the same, usually less. His figure 32 shows only the distal portion of the mandible and from an unfavorable viewpoint. Just behind the mandibles is the first pair of maxillae. Possibly this appendage is indicated in Krøyer's figure 5b of the mouth parts, a figure so singularly poor in details and yet a tribute to his ability to get so much from a single specimen and still have a whole type specimen left. It is probably also indicated, along with the second maxillae, in Pearse's enigmatic figure 29 *(cf. infra)*. Each maxilla is a conical structure bearing a blunt chitinous point on its end, with a tiny comb or rasp-like structure laterally, and a tiny thin projection medially. This latter in some specimens is curled somewhat like a shaving from a carpenter's plane. The appendage appears to have two articles but more probably there are three. The second maxillae, posterior to the first pair, are more massive and are, in my opinion, what Pearse (fig. 31) shows as second antennae. The resemblance between our figures is evident, although I have not been able to find the lateral setae on my specimens or on his. These appendages also, so far as I can determine, are composed of two articles each. The last of the mouth parts, the maxillipeds, are massive structures terminating in two processes. The exopodite bears 4 or 5 spines, the endopodite 1 or 2. My figure bears little resemblance to Pearse's figure of "second maxilliped (fig. 36)."

The pair of thoracic appendages (fig. 5), Pearse's "second legs," are relatively huge and so located as to suggest to the anthropomorphically-minded a pair of breasts. Each somewhat oval appendage ends in a pair of rami, the exopodite with 4 spines, the endopodite with 1 to 3 spines. My figure shows close agreement with Dr. Pearse's figure 30.

The shape of the body, as indicated above, is somewhat dependent upon the technique to which it is subjected in preparing the whole mounts. In the alcoholic specimens there are three well marked swellings along the dorsal surface, with a longitudinal ridge along each side. The single pair of thoracic appendages arises from these longitudinal swellings at the anterior end of the thorax. The abdomen is two-segmented and terminates in a pair of caudal rami. This is indicated in Krøyer's figure 5e, less well in Pearse's figure 35 and in my figure 7.

My figure of the male, figure 6, probably shows nothing not detectable in Krøyer's figure 5f, and he shows the articles of the two pairs of thoracic appendages more clearly than I have been able to make out. The male, although small, is evidently less degenerate than the female. Much of the segmentation persists; two pairs of thoracic and one pair of what appear to be degenerate abdominal appendages are present. The various sites where the males are found attached to the female suggest some ability to move about. The female lacks motor appendages, the holdfast organs and the thoracic appendages being adapted for anchoring her to a gill filament. The mouth parts are clearly adapted for rasping gill tissue to obtain blood. The parts are not adapted for blood sucking and I suspect that the blood pours into the mouth much as into a funnel. Although the male has mouth parts, I think it unlikely that it feeds. His little part on the stage of life is quickly played, and that done, there appears no good reason for his survival.

DISCUSSION

Reducing Dr. Pearse's new genus and species to a synonym requires some justification. Such taxonomic procedure, to make a profoundly unoriginal remark, is, in the last analysis, a matter of opinion. His slide, now No. 92,685 of the U.S. National Museum, has two labels on it in his handwriting. The left one has "*Tuccopsis pinguis* Pearse. 3 ♀♀ Type ♂," and the right one has "192. *Prionotus pectoralis* N. B. Breder. Port Aransas, Texas. Gills. A. S. Pearse." There is also an accession number, 192531, not in his handwriting. The specimens are mounted in what I suspect is polyvinyl alcohol. It would appear that he placed the several specimens in the mounting medium, dislodged the egg sacs and some of the debris, and then added the cover glass. Curiously, there are 5 specimens instead of the indicated 4, and all are females. The preparation is not in good condition, which from my own experience I would say is due to changes in the mounting medium. Some of the specimens may have shifted their positions somewhat. I have, therefore, had the opportunity of examining 5 of the 7 specimens he collected. The museum has another female which I have not seen. I think he must have dissected the remaining specimen. The smallest specimen, a female, is clearly the source of his figure 34, which he considered a male. The specimen from which he drew his figure 28 is recognizable if one assumes a slight turning of the specimen after the drawing was made. Likewise the source of his figure 30 is evident. I have already considered details of the appendages and given my interpretation of his figures of them and shall not repeat. Two of his figures remain for consideration. His figure 29 is not recognizable in any specimen on the slide, and hence I conclude it represents the specimen not otherwise accounted for and which he probably dissected. This ventral view of the head is not possible, so far as I understand it, without some teasing and distortion. The two pairs of what appear to be antennae in his figure can be only the two pairs of maxillae displaced far anteriorly. The roughly triangular mouth area is indicated, and the pair of maxillipeds appear in the lower portion of the figure. These are shown in a rather unfavorable view, especially so far as the distal portions are concerned. A bit of debris is indicated at their base. His figure 37 is still more difficult to understand and I have not seen any specimen of his or of mine in such a position as to suggest it. Possibly it is the headless body with the thoracic appendages left after his figure 29 was prepared, but I have not seen the bristles or setae he represents on any portion of the parasite's body.

Summarizing, Pearse's figures 28, 30, and 34 are readily recognizable from his slide, but 34 is a female and not a male. Figures 31, 32, 33, 35, and 36 are readily understood as presented, the differences I have indicated being due to the viewpoint or to interpretation. Figures 29 and 37 are at least enigmatical.

A critical point is the matter of the male. Pearse's type ♂ is a female, as already pointed out, smaller and without egg strings. A search of his slide discloses two pygmy males, one associated with an egg string and one free in the debris. It would be relatively easy to detach a male as the egg strings were removed, and likewise to dislodge one while trying to remove the detritus and so get a better view of the female. Neither is a good specimen and I suspect would be overlooked unless one were searching for them. I think he actually indicates a male in his figure 28, where an oval body is drawn at the origin of the egg strings. After examining the specimen from which the drawing was made I am convinced that it is a male. It could, of course, be a representation of the abdomen. The specimen would have to be reworked to establish this beyond question.

In the same paper Pearse records as *Tucca sp.* details of two mutilated specimens, one from the smooth swellfish *(Lagocephalus laevigatus)* and one from the crimson sea robin *(Prionotus ophryas)*. The size is within the range of *Blias prionoti*, the general shape of the body is similar, and some of the details given are suggestive, *e.g.*, "the mandibles are 3-segmented, rather stout, the terminal segment forming a *slightly curved hook* (italics mine)." The mandible of *B. prionoti* may look that way. Most suggestive are the "two slender rods are embedded and extend forward on either side" from a mutilated head. *B. prionoti* often looks that way when pulled away from the gill filament. In my opinion his *Tucca sp.* specimens were mutilated *B. prionoti*, and Dr. Pearse was the first to see the holdfast organs reported in this paper.

This is a difficult copepod to work with. The mucus and associated debris are difficult to impossible to remove, especially in the areas where the appendages are, and the critical mouth parts are so small. I have been fortunate in having an abundance of material to work with. Nothing in this paper should be taken as more than a difference of interpretation between Dr. Pearse and me for he has been a longtime friend and counselor and, if his present health permitted him to read this manuscript as he has my previous copepod papers, I have little doubt that it would come back with his famous "Hell's Bells" written on it in big letters and a generous word.

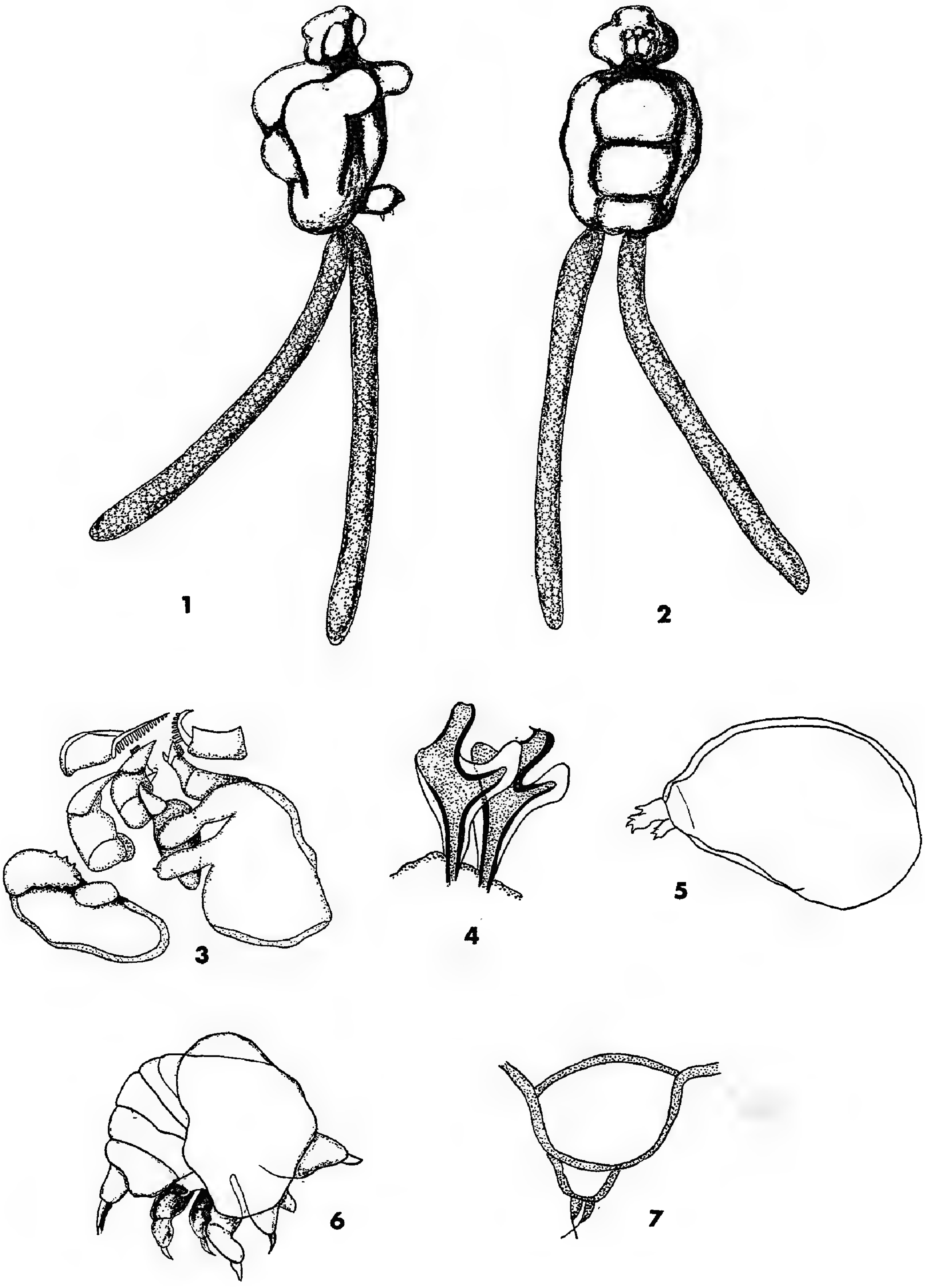

Fig. 1, lateral view of female and attached male; Fig. 2, dorsal view of same female; Fig. 3, mouth parts; Fig. 4, chitinous holdfast organs of head; Fig. 5, a left maxilliped; Fig. 6, male; Fig. 7, abdomen and caudal rami.

A Contribution to the Hydrography of Apalachicola Bay, Florida

By

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INTRODUCTION

The study of estuarine hydrography has increased considerably in recent years and a number of surveys have been conducted on various estuaries of the Atlantic and Pacific coasts. These investigations have been mainly concerned with relatively deep systems which cannot be compared with shoal embayments associated with estuarine areas of the Gulf of Mexico. Recent studies of Gulf coast estuaries are confined to those of Collier and Hedgpeth (1950) on the Texas bays and Austin's report (1954) on Mobile Bay. Comprehensive investigations of west Florida estuaries have not been made.

This paper is presented as a contribution to the hydrography of Apalachicola Bay, with particular reference to observed surface salinity and temperature conditions during the period from August 1953 through August 1954. Field data upon which this study is based were collected in the course of oyster investigations supported by the Florida State Board of Conservation.

During the early summer of 1953 a sampling program covering a relatively large number of stations was initiated in an effort to obtain knowledge of salinity and temperature conditions in Apalachicola Bay. The establishment and continuation of this study was further prompted by the imminent dredging of a boat channel through St. George Island and the approaching completion of the Jim Woodruff Dam on the Apalachicola River at Chattahoochee, Florida. Each of these projects was expected to modify the natural hydrographic conditions and the cumulative result could, conceivably, be detrimental to the commercial oyster population of the area.

Too often man-made changes in the natural features of estuarine areas have been undertaken, some of them useless or unnecessary, without thought being given to the effects such works may have upon the hydrography and fishery resources of the region. The biologist investigating the fisheries of such an area, after the fact, must perforce rely upon the casual and usually inaccurate recollections of local inhabitants for information on conditions prevailing prior to such construction.

Previous long-term salinity and temperature studies in Apalachicola Bay (Ingle and Dawson, 1951) were confined to a maximum of thirteen stations. These observations showed that weekly and long term salinity variations of 10 or 15 ‰ were not uncommon, but they did not permit any more than general assumptions regarding salinity distribution throughout the bay. Neither was it possible to substantiate any ideas regarding the effects of wind and river stage on the overall salinity pattern. The material presented here, therefore, represents a final study of the natural hydrographic conditions in Apalachicola Bay prior to the completion of the aforementioned projects.

The author is indebted to the U. S. Geological Survey for unpublished data on river discharge and to Mrs. H. Griswold, Messrs. Joe Martina, Jr., and R. W. Wing for their active assistance and cooperation during the field phase of this study.

METHODS

From August 1953 through August 1954 surface salinity and temperature observations were obtained from ninety stations in Apalachicola Bay. Stations were chosen to give as wide a coverage of the area as possible and yet remain within practical limits. Many stations coincided with sites previously established by the Florida State Board of

Health as bacteriological sampling stations. All were located by reference to navigational aids or by triangulation on known landmarks.

Although observations are sparse at several of the more inaccessible locations, every effort was made to obtain frequent samples. Circumstances did not permit the establishment of a definite sampling schedule. Except for five stations accessible from the shore, sampling was conducted from a fast launch or speedboat and from ten to seventy-nine stations were visited in a single day. With an average of eight sampling days per month, this study includes data obtained on one hundred and six sampling days. The number of sampling days and the number of samples collected per month are shown in Table 1.

TABLE 1

Sample Distribution During Survey Period.

Month	Sampling Days	Salinity Samples	Temperature Samples
August, 1953	4	42	26
September	2	26	....
October	5	68	....
November	6	106	....
December	5	103	25
January, 1954	7	127	68
February	13	234	206
March	12	254	234
April	13	334	303
May	11	235	161
June	8	115	82
July	9	160	139
August	11	169	149
Total	106	1,973	1,393

All salinities were determined in the laboratory with sea water hydrometers.

Surface water temperatures were determined *in situ* with a Gemware surface thermometer. No temperatures were obtained during September, October and November. Since there was little variation in surface temperatures between stations on any sampling day, temperatures were not always taken at every station visited.

DESCRIPTION OF AREA

a) Apalachicola Bay

The waters covered in this study are located on the northeastern coast of the Gulf of Mexico in Franklin and Gulf counties, Florida. They include East Bay, Indian Lagoon, St. Vincent Sound, Apalachicola Bay and the western portion of St. George Sound (Fig. 1).

East Bay is more or less landlocked on three sides and the John Gorrie Bridge, joining Apalachicola and East Point, may be taken as the southern boundary. The east-west limits of the remaining units (Indian Lagoon, St. Vincent Sound, Apalachicola Bay and western St. George Sound) have not been adequately defined. For present purposes, therefore, these waters will be treated as a single unit, Alapachicola Bay. This area extends from the east end of St. George Island to the head of Indian Lagoon. Bounded on the north by the mainland and East Bay, it is separated from the Gulf of Mexico on the south by Indian Peninsula, St. Vincent Island and St. George Island.

Two natural openings, Indian Pass and West Pass, provide access to the Gulf through these barrier islands. The passes are relatively deep but shifting offshore bars limit their

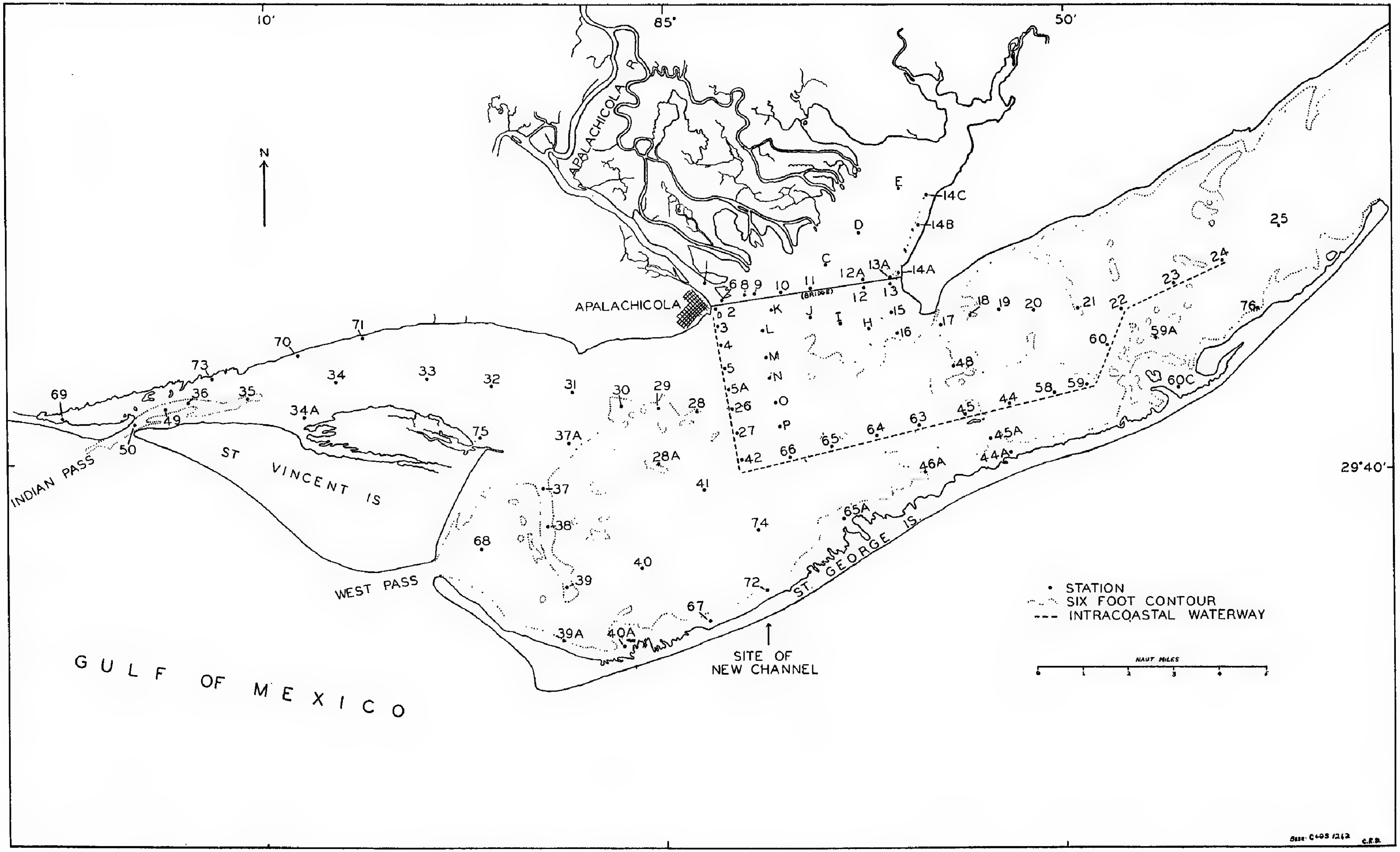

10'
85°
50'
29°40'
N
APALACHICOLA R.
APALACHICOLA
(BRIDGE)
INDIAN PASS
ST VINCENT IS
WEST PASS
ST. GEORGE IS.
GULF OF MEXICO
SITE OF NEW CHANNEL
• STATION
SIX FOOT CONTOUR
INTRACOASTAL WATERWAY
NAUT. MILES
0 1 2 3 4 5
1 2 3 4 5 5A 6 8 9 10 11 12 12A 13 13A 14A 14B 14C 15 16 17 18 19 20 21 22 23 24 25 26 27 28 28A 29 30 31 32 33 34 34A 35 36 37 37A 38 39 39A 40 40A 41 42 44 44A 45 45A 46A 48 49 50 58 59 59A 60 60C 63 64 65 65A 66 67 68 69 70 71 72 73 74 75 76
C D E H I J K L M N O P

Fig. 1. Chart of Apalachicola Bay showing station locations, the six foot contour, and the site of the newly dredged boat channel.

use to shallow-draft vessels. A dredged channel was completed through St. George Island, approximately 8.4 miles east of West Pass, at the end of August, 1954. This has not been jettied, but it is understood that it will be maintained indefinitely as a small boat channel.[1] It is of interest to note that two separate natural channels, Sand Pass and New Inlet, which previously opened through St. George Island to the west of this new cut have been completely filled in, presumably as a result of hurricanes, since they were charted by Swift in 1896.

The eastern extremity of Apalachicola Bay is approximately 4.5 miles wide and here free exchange of water is not restricted by bars or shallows of any magnitude.

The entire system is relatively shallow and averages approximately 5 feet deep at MLW. Extensive shoals and shallows are present along much of the shoreline, and, in some cases, these extend well out into the bay. Such shoals are frequently exposed during the winter northers, and, to a lesser extent, during low water spring tides. Reference to the depth contours (Fig. 1) will show that there are a number of bars and lumps scattered throughout the area. Depths in excess of 15 feet are, in general, restricted to the passes and a few channels between oyster bars.

The delta of the Apalachicola River is located about midway along the northern shore of the bay. The principal distributary flows into the bay at Apalachicola, and a number of subsidiary streams open into East Bay. This river is the major source of fresh water for the system and is discussed at greater length below.

Apalachicola Bay may be described as a shallow coastal plain estuary, oriented in an east-west direction, protected by a string of barrier islands and supplied with fresh water by the Apalachicola River. Further descriptive data are presented in Table 2. Although the figures are calculated from nautical charts, they should be regarded as approximations of the exact measurements.

TABLE 2

Descriptive Data on Apalachicola Bay and Associated Areas. Unless Otherwise Stated, All Measurements are in Statute Miles.

	Apalachicola Bay	East Bay	Indian Pass	West Pass	Dredged Channel
Length	35.1	9.2	......	......	......
Max. Width	8.1	4.8	......	......	......
Min. Width	0.1	0.1	400*	800*	100*
Avr. Width	5.0	2.0	......	......	......
Circumference	110.0	35.0	......	......	......
Area; sq. mile	130.0	13.0	......	......	......
Max. Depth; ft. MLW	33	23	24	40	......
Avr. Depth; ft. MLW	5	3	......	......	10†

* Yards.
† Controlling depth.

b) Climatic factors and tides

Mean annual precipitation for the City of Apalachicola during the period of record, 1922 through 1953, is 56.29 inches, with highest rainfall commonly occurring during July, August and September.

---

[1] I have been recently notified, personal communication from Mr. R. W. Wing, that an offshore bar has formed and that the new cut is impassible at this time. It is understood that the pass will be reopened and jettied in the near future.

In order to obtain a mean total precipitation figure for a thirteen-month period comparable to that of the present study, the mean August rainfall has been added to that of the annual mean. The average precipitation for the thirteen months over the station record is, therefore, 63.83 inches. Total precipitation during the corresponding period in 1953–1954 was 64.11 inches or 0.28 inches in excess of the mean. Monthly distribution of rainfall is shown in Figure 2. High rainfall for September, 1953, was a consequence of a small tropical disturbance which passed inland to the west of Apalachicola on September 26th. Rainfall was above normal during November and December, but the period from January through May and the month of August, 1954, were significantly deficient in comparison to the station means.

During the "rainy season," June through September, sudden downpours are common. At such times local runoff may result in pronounced temporary reductions in inshore surface salinities.

Apalachicola enjoys a mean annual precipitation considerably greater than the 26 to 30 inches reported for the Aransas system by Collier and Hedgpeth (1950), but roughly nine inches less than the 65 inches that Austin (1954) records for the Mobile area.

It has been previously stated that easterly winds prevail at Apalachicola (Ingle, 1951; Ingle and Dawson, 1953). Examination of the 23 year record of observations (Fig. 3A) shows that, in per cent of time, there is an almost equal distribution between winds of the easterly and northerly quadrants with northerlies being one per cent the more frequent. From August 1953 through August 1954, northerly winds occurred 49 per cent of the time, whereas easterly winds were experienced but 25 per cent of the time (Fig. 3B).

The station mean wind velocity is 8.2 m.p.h., and calms occur less than 0.5 per cent of the time. The maximum recorded velocity, 67 m.p.h., occurred in September, 1947. Monthly average and maximum velocities, and the monthly prevailing direction during the study period are shown in Figure 3C.

Northerly winds are normally most frequent during the months from September through February; winds from southerly quadrants are most common during the remainder of the year.

There is no tide gaging station in Apalachicola Bay. Predicted tide ranges are given in the Tide Tables for four stations as shown in Table 3. On the basis of predicted time differences, the tides at Apalachicola and Cat Point are, respectively, 25 minutes later and 30 minutes earlier than at West Pass.

TABLE 3

Predicted Tide Ranges for Apalachicola Bay.

Tide Station	Survey Station	Mean Range in Ft.	Spring Range in Ft.
Cat Point	17	1.3	1.7
Apalachicola	2	1.0	1.3
Lower Anchorage	39A	0.9	1.2
West Pass	68	0.8	1.0

The effect of wind on water levels in Apalachicola Bay is pronounced, and may frequently exert greater influence than the astronomical tide. During a norther there may be little or no observable flood tide and bay water levels may be reduced by a foot or more. At such times, normally shoal areas are exposed for long periods. Southerly winds augment the astronomical tides and often result in abnormally high water without an observable ebb. These effects occur gradually with moderate wind velocities, and results may not be immediately noticeable. With fresh winds, however, there is a rapid change in the normal tidal pattern and the damping or cumulative effects of the wind are often evident within two or three hours after the wind shift.

Similar shifts in water levels, under the influence of northers, have been reported for both Mobile Bay and the Texas bays. Due to the lack of tide gages suitable records

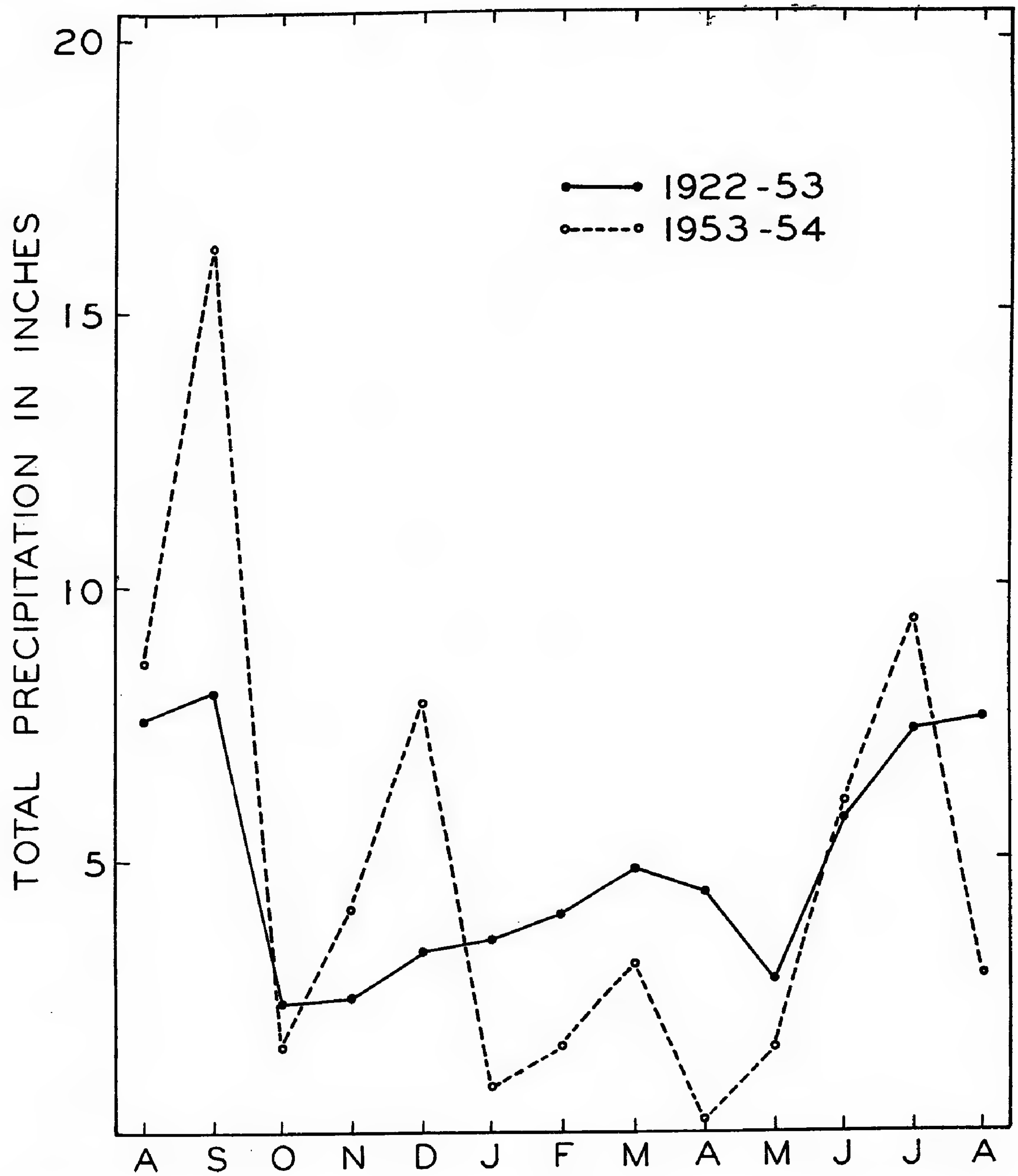


FIG. 2. Total monthly precipitation at Apalachicola, 1953–1954, as compared with average monthly total precipitation over the station record, 1922–1953.

are not available which would show whether seiches, such as occur in the Aransas system, accompany radical wind shifts at Apalachicola. If such oscillations take place in the area, they appear to be of little amplitude for direct observation has so far not revealed them.

A flood stage in the Apalachicola River may serve to obscure tidal effects near the delta, but this influence was not observable either in the open bay or at reasonable distances to the east and west of the delta during the survey period.

The mean annual air temperature at Apalachicola is 68.7° F., with maximum and minimum temperatures of 102.0° F. and 18.0° F., respectively, over the thirty-one year station record (1921–1952). Maxima occur during July and August and the lowest tem-

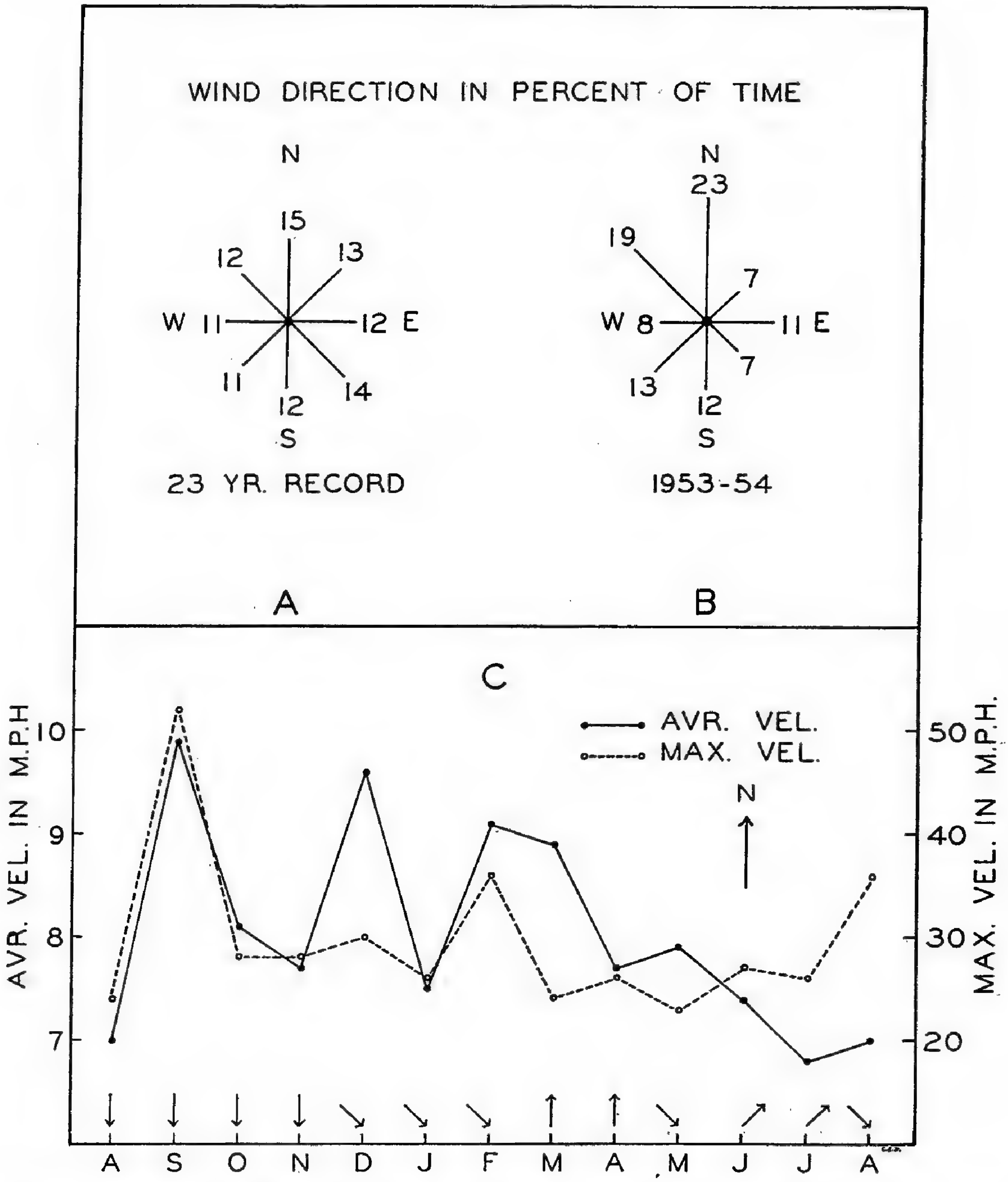


FIG. 3. a). Wind directions, in per cent of time, at Apalachicola over a 23 year period; b). Wind directions at Apalachicola, in per cent of time, August 1953 through August 1954; c). Monthly average and maximum wind velocities and monthly prevailing direction, 1953–1954.

peratures come during January. Freezes are not uncommon, but such lows seldom extend over more than a two or three day period. Mean monthly air temperatures over the 1921–1950 record and during the 1953–1954 study period are shown in Figure 4.

c) Drainage Basin

The Apalachicola River is the principal source of fresh water for Apalachicola Bay. Together with its main tributaries, the Chattahoochee, Flint and Chipola rivers, it drains parts of Florida, southeast Alabama and much of western Georgia (Fig. 5).

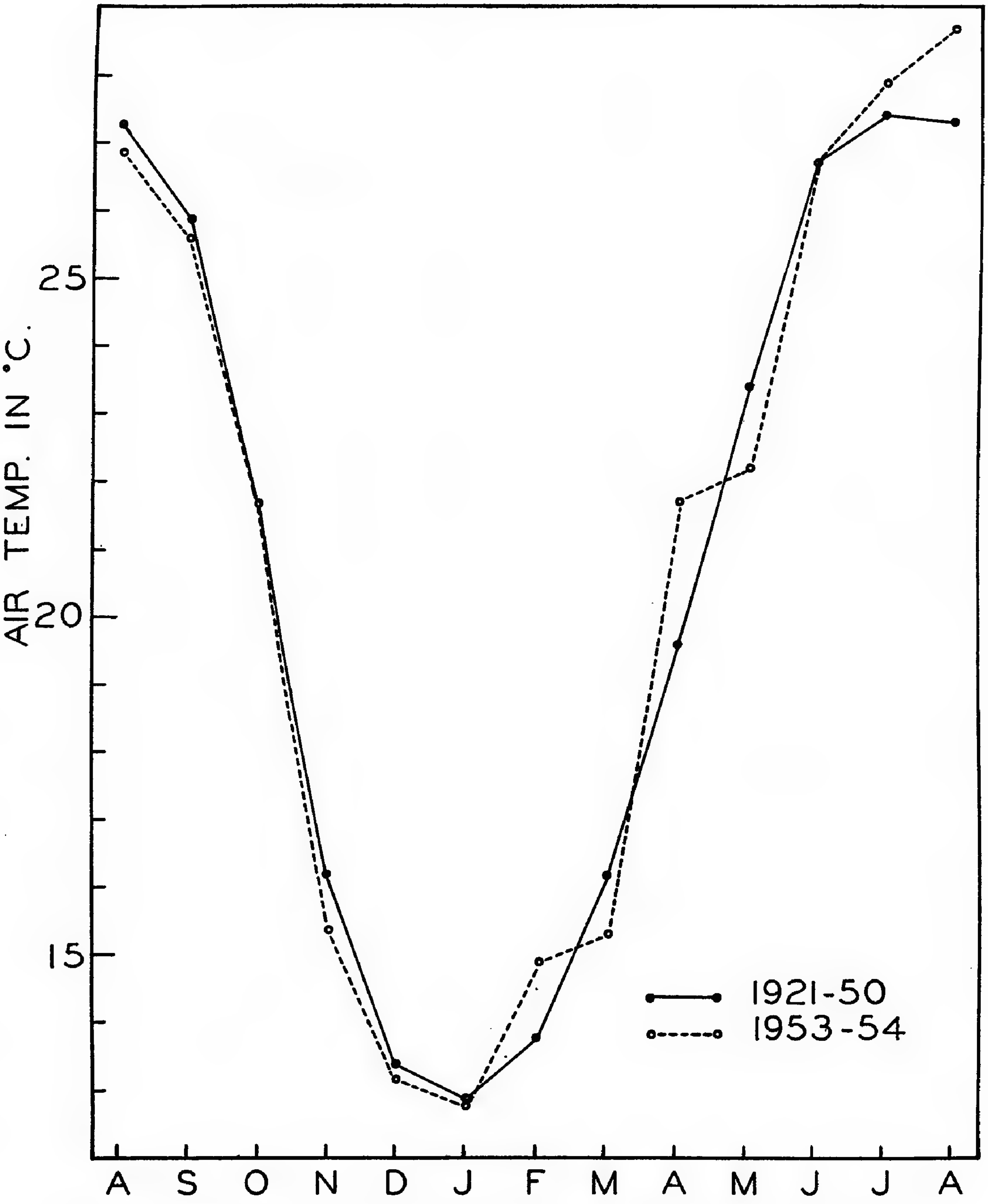
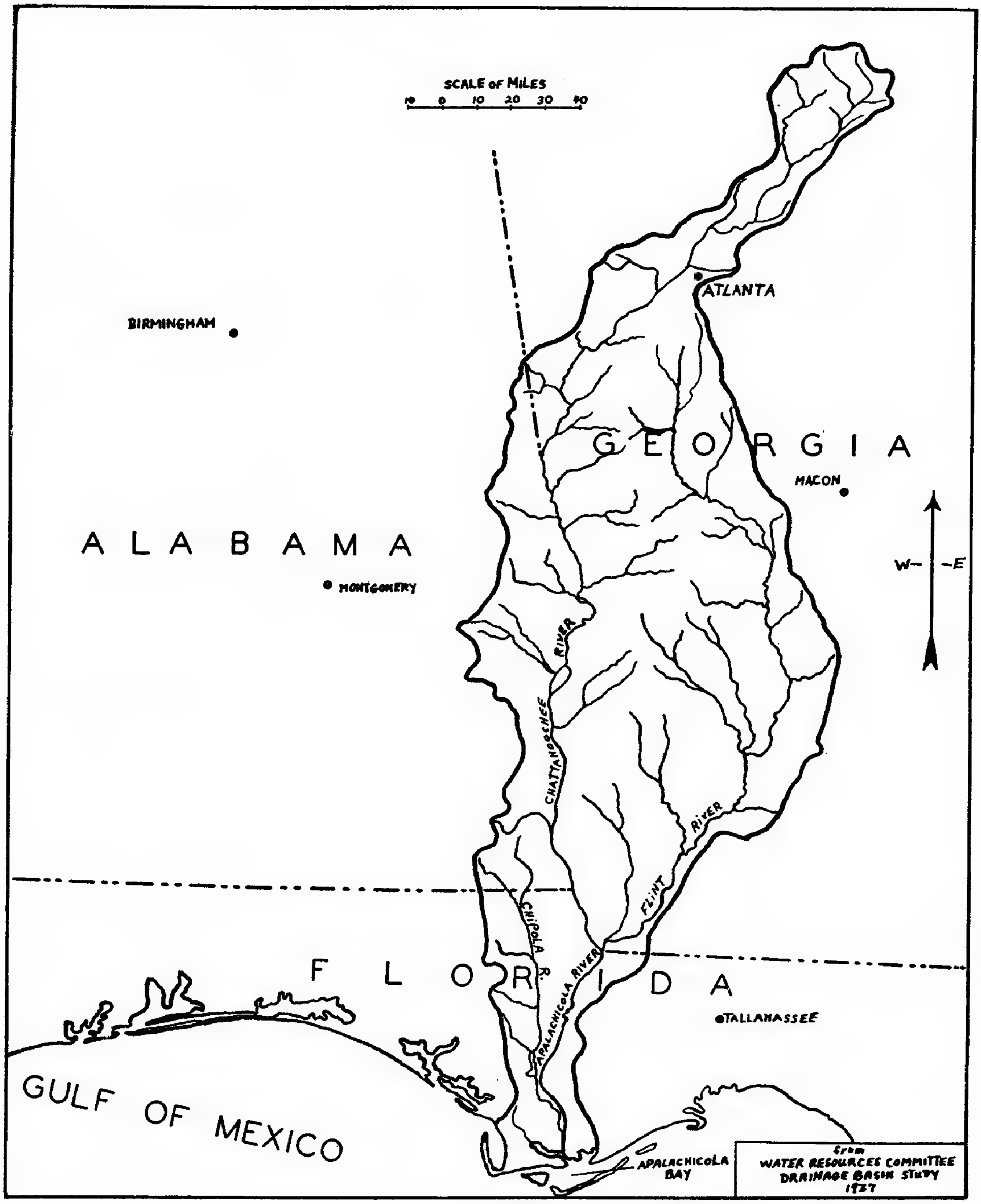


Fig. 4. Mean monthly air temperature at Apalachicola 1921–1950, and August 1953 through August 1954.

The drainage basin is about 400 miles long, and includes approximately 19,500 square miles.

The Chattahoochee River originates in Union County, Georgia, not far from the South Carolina line. For much of its course it forms the boundary between Georgia and Alabama before flowing into the Apalachicola River at Chattahoochee, Florida. The source of the Flint River is in Fulton County near Atlanta, Georgia, and it also joins the Apalachicola at Chattahoochee. The Chipola River, beginning in Houston County


SCALE OF MILES
10 0 10 20 30 40
ATLANTA
BIRMINGHAM
GEORGIA
MACON
W
E
ALABAMA
MONTGOMERY
CHATTAHOOCHEE RIVER
FLINT RIVER
CHIPOLA R.
APALACHICOLA RIVER
FLORIDA
TALLAHASSEE
GULF OF MEXICO
APALACHICOLA BAY

from WATER RESOURCES COMMITTEE DRAINAGE BASIN STUDY 1937

Fig. 5. Apalachicola drainage basin, diagrammatic, improvements not shown.

at the southeast corner of Alabama, joins the Apalachicola River approximately thirty miles upstream from the city of Apalachicola.

The Jim Woodruff Dam now under construction at Chattahoochee, Florida, near the confluence of the Flint and Chattahoochee rivers is a multiple purpose project designed for navigational and hydroelectric functions. The impounded reservoir will include some 37,500 acres and will have a maximum capacity of 385,000 acre-feet. The latest available information indicates that filling of the reservoir will not begin until the latter half of 1956. Under conditions of normal river stage, it is expected to take from two to four weeks to fill the reservoir; during which time the flow past the dam will be reduced to 5,120 cfs. This corresponds to the minimum recorded flow at the Chattahoochee gaging station. Navigational requirements will limit variation in reservoir level to a maximum of one foot.

There is no gaging station at the town of Apalachicola, but stations are maintained by the United States Geological Survey at Chattahoochee, below the confluence of the Flint and Chattahoochee rivers, and on the Chipola River at Altha, Florida. A relatively accurate estimate of the discharge at the mouth of the Apalachicola may be obtained by increasing the sum of the Chattahoochee and Altha discharges by ten percent. By using this method and data over the station record at the two localities, the mean monthly discharge at Apalachicola is estimated at 25,969 cfs. Mean monthly discharges at Chattahoochee and Altha during the study period, obtained from unpublished records of the Geological Survey, are shown together with the estimated discharge at Apalachicola in Figure 6. The low discharge recorded for August, 1954, reflects the drought conditions existing in Georgia and northwest Florida, and approximates the estimated minimum recorded flow of 6,200 cfs. at Apalachicola.

DATA AND DISCUSSION

Thirteen hundred and ninety-three surface water temperatures were obtained during the sampling period. The monthly means and ranges, for all stations, are shown in Table 4 together with the monthly average air temperatures over the station record (1921–1950) and the sample period.

Water temperatures in Apalachicola Bay closely parallel air temperatures with highest recordings during July and August and a January minimum. The relationship between air and water temperatures is shown in Figure 7 by the method of Roelofs and Bumpus, (1953). The mean of water temperatures observed during a sampling day is plotted against the average air temperature of the sampling day and the day previous. This makes allowance for lag in water temperature. The coefficient of correlation between these air and water temperatures is 0.961, and well within the one per cent level of significance.

Collier (1938) and Collier and Hedgpeth (1950) showed a similar parallelism between air and water temperatures in Aransas and Copano bays, Texas, and reported an annual range of water temperature averages for these bays as 13.5° C. and 16.5° C., respectively.

The 18.1° C. range in the monthly averages at Apalachicola during the survey is considered to be unusual and is mainly due to the abnormally high air temperatures experienced during July and August, 1954. The normal annual range of monthly average water temperatures is probably on the order of 16.5° C.

Daily variation in surface temperature over the sampling area averaged less than 2.0° C., and much of this is ascribed to the effects of insolation. Abnormally high or low temperatures were frequently observed in shoal areas during low water, but such local extremes were rapidly modified with the flood of the tide.

Although freezes are not infrequent at Apalachicola, mass mortalities of fishes and invertebrates such as occur in the Texas bays (Gunter, 1941; Gunter and Hildebrand, 1951) and on the lower west coast of Florida (Storey and Gudger, 1936) have not been recorded in these waters.

Due to the shallow character of the basin and the pronounced effect of wind on the bay waters there is little thermal stratification in Apalachicola Bay. A number of observations

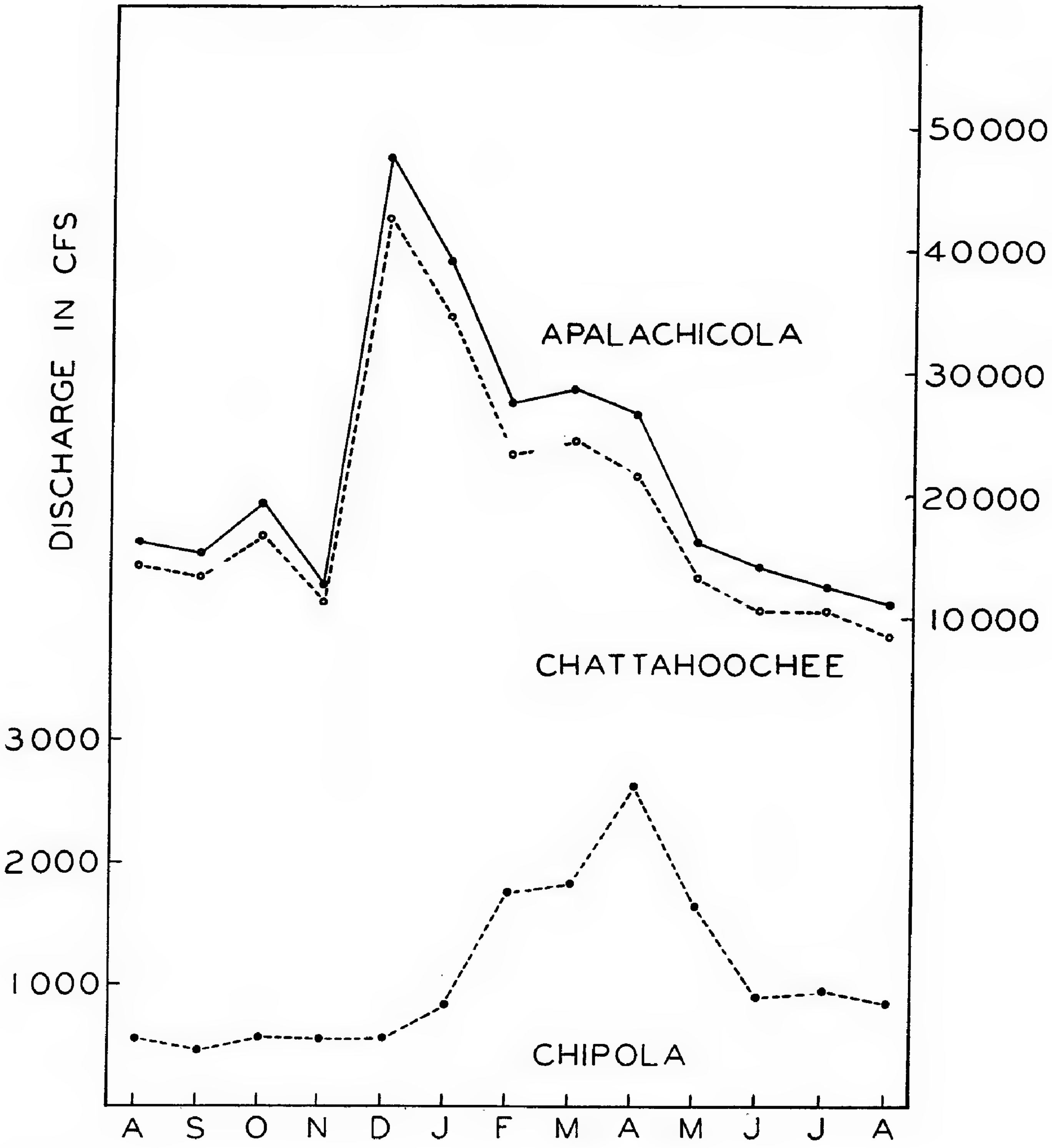


Fig. 6. Recorded mean monthly river discharge at Chattahoochee and Altha and estimated mean monthly discharge at Apalachicola.

in the open bay have shown that differences between surface and bottom temperatures average less than 1.0° C. Pronounced variation between surface and bottom temperatures may occur in the deeper holes and at the river mouth, but no data are available.

Nineteen hundred and seventy-three salinity samples were collected from ninety stations (see Fig. 1) during the survey period. The data obtained at each station is summarized in Table 5.

From observations at a limited number of stations, it was previously shown (Ingle and Dawson, 1951) that certain areas of Apalachicola Bay were subject to wide and rapid variations in surface salinities. The present data show that weekly and long term variations of considerable magnitude occur throughout the bay. Long term variations

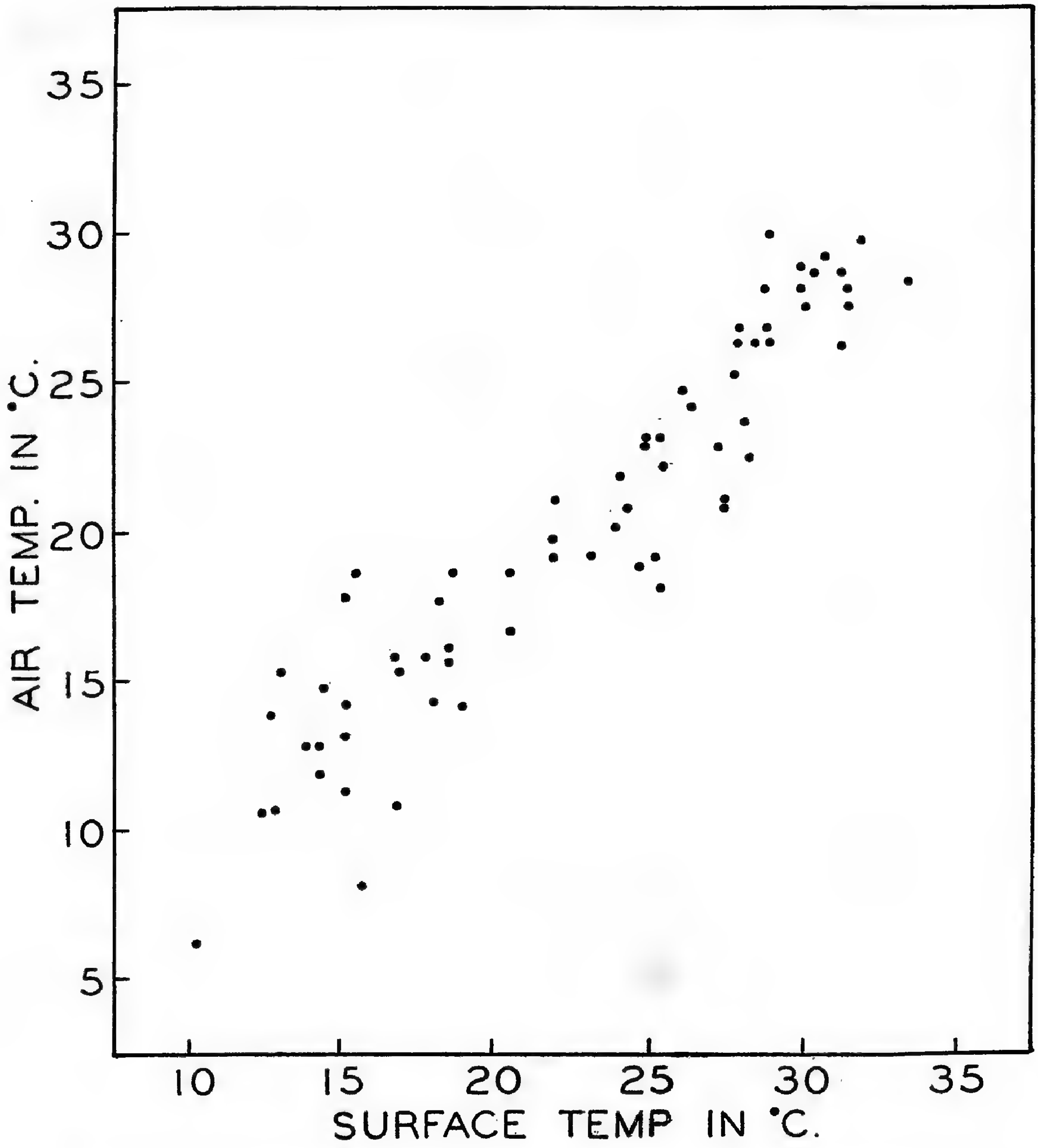


Fig. 7. Relationship between water temperatures of Apalachicola Bay and air temperatures at Apalachicola.

of 25 ‰ or more were found at fifty-two stations, and mean weekly ranges of more than 10 ‰ were recorded at eight stations. Such fluctuations result from the cumulative effects of river discharge, wind direction and velocity, local run-off and tide stage. Of these, local run-off is probably the least significant in that its measurable effects are usually transient and, except under unusual circumstances, confined to waters adjacent to the shore.

No data on salinity variation during the tidal cycle were obtained during 1953–1954. A number of observations were made during the previous investigation, and tidal variations of as much as 15 ‰ were reported (Ingle and Dawson, 1951). Considered in the light of present knowledge of the effects of wind on the movement of water masses within the bay, salinity variations of such magnitude cannot be ascribed entirely to tidal movements. Although no data are presented here, it is commonly accepted by watermen along the Florida West coast that wind shifts often occur on the change of the tide. This factor, together with variations in velocity during the sampling period could introduce variables, previously not recognized, which prevent the assignment of the so-called "tidal" variations to the astronomical tides. It should, however, be recognized that the magnitude of tidal variations can be expected to vary spatially with the change in river discharge. With high discharge, tidal effects are minimized over much of the Bay, but during periods of low water pronounced tidal variations may be expected at the mouth of the river and in East Bay.

TABLE 4

Monthly Water Temperature Means and Ranges Compared with Monthly Mean Air Temperatures of the Station Record at Apalachicola (1921–1950) and Sample Period.

	Water		Air	
Month	Range ° C.	Mean ° C.	Station Record ° C. 1921–1950	1953–1954 ° C.
August	26.0–29.0	27.6	27.3	26.9
September			25.9	25.6
October			21.7	21.7
November			16.2	15.4
December	11.5–19.0	13.5	13.4	13.2
January	9.5–15.0	12.7	12.9	12.8
February	12.7–21.3	16.1	13.8	14.9
March	11.4–26.0	15.8	16.2	15.3
April	19.9–32.0	25.1	19.2	21.7
May	19.4–29.4	24.1	23.4	22.2
June	27.3–30.0	28.6	26.7	26.7
July	27.2–35.0	30.8	27.4	27.9
August	28.8–33.0	30.7	27.3	28.8

As noted above, the wind exerts a major influence on the waters of Apalachicola Bay with respect to water levels and mass movements. Although fluctuations in discharge rate and the lack of calms make it impossible to arrive at a "normal" condition for the area, an estimate of the effects of wind can be obtained by comparing observations made at similar river levels when winds were from different directions. Such a comparison is presented in Figure 8. On February 11, 1954, southwesterly winds directed the river flow to the east while high salinity Gulf water entered the bay through Indian Pass and West Pass. Southeasterly winds of April 14, 1954, resulted in a westerly movement of low salinity water toward West Pass and Indian Pass, and the inflow of high salinity water through the eastern end of the Bay. Although less pronounced, examination of the mean

TABLE 5

Summary of Salinity Observations at each station during the Survey Period.

Station	August 1953–August 1954					Weekly	
	No. Obs.	Sal. Range in ‰	Mean Sal. in ‰	σ	No. Obs.	Max. Range in ‰	Mean Range in ‰
1	11	0.8– 5.0	2.7	1.2	1	2.1– 4.5	2.4
2	27	0.8– 9.6	3.6	2.2	17	2.2– 7.1	1.4
3	39	0.7–10.2	3.5	2.4	27	7.3– 1.2	1.7
4	53	0.0–17.6	4.0	4.2	38	5.4–16.0	2.2
5	59	0.0–24.4	6.6	7.0	43	5.2–24.4	3.9
5A	29	1.8–34.4	14.3	8.8	22	9.6–24.0	5.9
6	30	0.7–16.2	4.0	3.3	19	16.2– 3.3	2.6
8	27	0.9–10.8	4.9	3.0	20	10.8– 2.8	2.4
9	48	0.7–20.4	5.9	5.0	28	11.4– 1.3	2.9
10	9	1.3–18.4	5.7	5.4	4	4.1–18.3	6.0
11	44	0.3–25.6	7.4	6.2	25	25.6– 2.6	4.4
12	7	0.4–16.0	5.0	5.2	...	....	......
12A	43	0.4–38.9	9.9	8.0	25	38.9– 7.2	6.9
13	40	0.4–38.9	14.0	10.5	23	9.8–38.9	10.6
13A	45	0.4–29.3	9.9	7.7	27	4.6–29.3	7.7
14A	11	3.3–21.2	11.9	6.7	3	15.2– 5.5	8.0
14B	10	3.0–25.9	14.1	8.5	3	24.7– 6.2	12.3
14C	8	2.5–23.7	12.8	8.1	1	23.7–11.1	12.6
15	41	0.4–39.9	17.2	11.9	20	7.6–37.1	10.6
16	53	0.8–40.6	17.4	11.6	33	38.4– 7.2	11.3
17	26	1.2–37.5	17.7	10.2	6	25.1–10.2	4.8
18	16	0.5–26.6	14.0	8.4	3	25.1–12.8	6.6
19	16	1.8–28.4	15.5	8.3	3	27.9–16.3	6.3
20	15	1.8–28.4	15.5	7.6	3	29.3–19.8	5.3
21	15	3.9–29.8	17.7	7.8	3	30.4–20.3	5.5
22	15	5.6–31.6	19.0	7.3	3	30.6–22.2	5.1
23	9	11.2–26.7	21.5	5.5	2	17.6–22.9	4.7
24	9	10.3–29.5	20.9	5.5	2	18.2–24.8	6.5
25	9	10.0–29.2	23.6	6.3	2	17.9–28.7	6.1
26	59	0.1–35.0	11.7	9.0	40	29.8– 9.0	4.6
27	41	0.1–31.9	13.5	10.4	22	7.9–20.6	5.2
28	34	0.7–25.1	8.6	7.6	23	25.1–13.4	3.2
28A	6	7.7–26.4	16.7	6.8	....	....	......
29	35	1.1–22.8	9.5	7.2	22	6.2–21.9	4.1
30	35	1.8–26.1	10.9	7.5	20	4.7–15.8	4.2
31	35	1.3–29.3	14.1	7.9	20	25.7–15.3	4.2
32	19	5.3–31.3	14.1	7.5	3	5.3– 9.5	2.2
33	16	5.7–35.2	15.4	8.6	3	5.7–11.9	3.3
34	15	5.5–36.0	19.5	9.6	3	18.3–17.4	0.8
34A	7	6.7–33.7	17.4	8.8	1	11.1– 9.5	1.6
35	9	10.1–36.0	24.5	9.0	1	13.6–10.1	3.5
36	6	10.1–34.9	22.0	8.4	1	15.3–10.1	5.2
37	17	4.1–35.1	13.5	9.6	5	32.9–12.5	6.1
37A	19	3.7–30.3	13.2	8.5	7	30.3–18.5	3.9
38	17	3.5–35.6	15.8	9.4	4	35.4–21.8	4.3
39	15	4.2–35.1	18.1	9.8	4	35.1–20.7	4.9
39A	16	4.6–34.9	18.9	9.4	4	34.9–19.5	5.4
40	13	2.4–26.0	12.7	8.3	3	2.4–12.0	6.4
40A	12	10.0–35.0	20.9	7.8	3	35.0–23.4	8.6
41	15	1.7–41.9	13.6	10.3	2	10.9– 8.4	1.8
42	41	0.4–39.8	15.9	9.9	20	32.9–12.7	4.9
44	16	3.9–28.5	16.2	7.3	6	15.1–28.5	5.6
44A	14	9.8–38.4	19.0	8.1	6	24.3–11.3	7.3
45	26	1.1–39.2	18.1	9.5	10	7.2–23.9	6.1
45A	13	0.7–38.9	18.6	9.7	4	24.5–11.5	7.6
46A	16	0.8–38.1	19.3	11.6	4	23.5– 6.0	10.1
48	23	1.2–41.0	19.7	12.1	8	37.3– 7.6	14.3
49	7	12.1–36.0	27.1	8.1	2	21.8–12.1	8.4
50	37	10.6–36.4	27.6	8.5	27	10.6–33.3	7.3
58	16	4.2–29.9	17.2	7.6	6	15.7–29.9	5.6
59	17	3.4–30.6	18.2	7.8	6	14.4–29.5	5.6
60	12	4.2–31.2	19.2	8.0	3	30.8–21.6	4.5

TABLE 5 *(Continued)*

Summary of Salinity Observations at each station during the Survey Period.

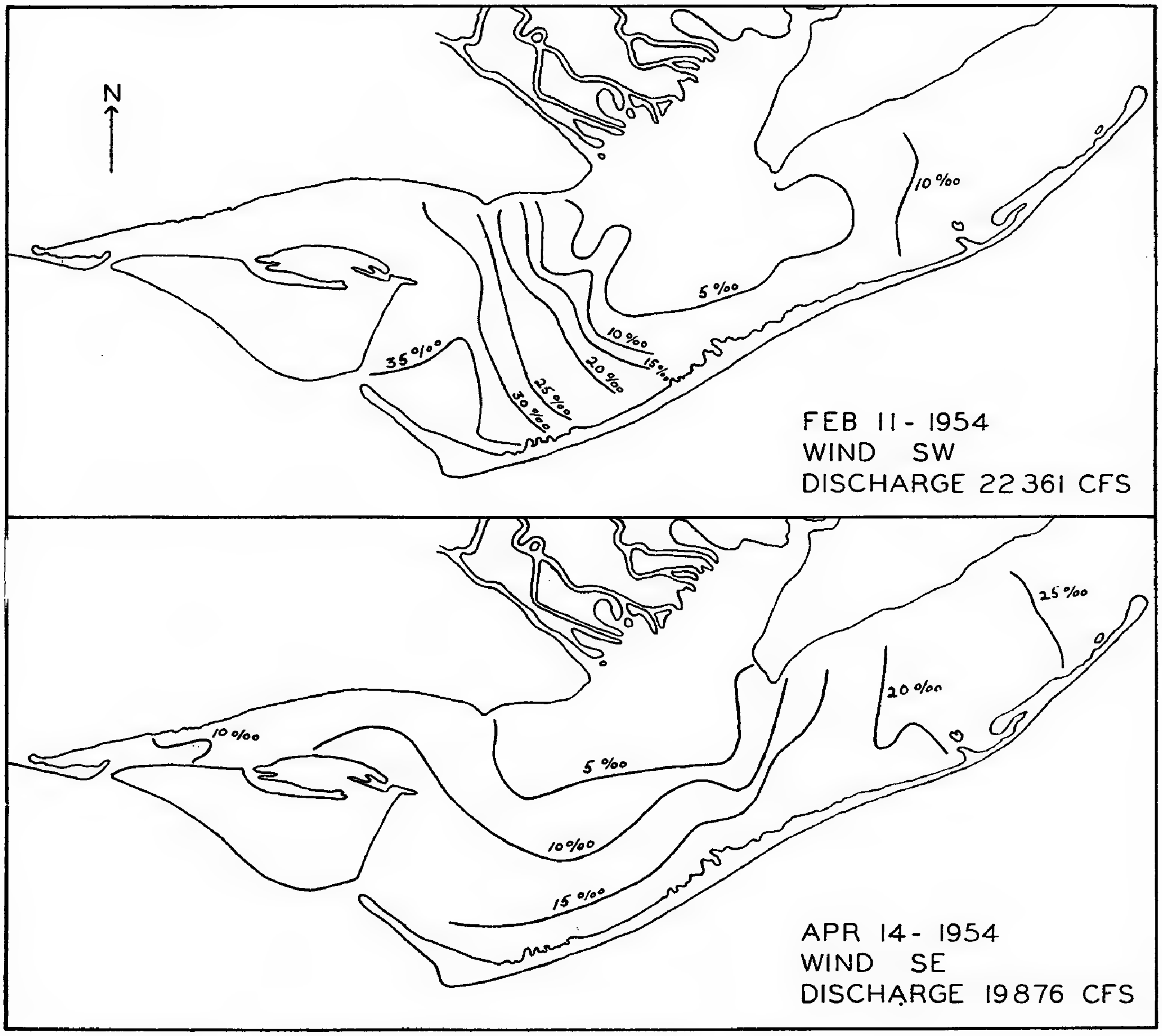
	August 1953–August 1954						
Station	**No. Obs.**	**Sal. Range in ‰**	**Mean Sal. in ‰**	σ	**No. Obs.**	**Weekly Max. Range in ‰**	**Mean Range in ‰**
60C	8	13.8–28.0	21.8	4.6	2	15.6–26.1	6.8
63	29	0.5–38.9	16.4	11.6	13	38.9– 4.1	8.4
64	29	0.3–38.6	15.8	11.5	11	38.6–17.0	7.5
65	30	0.5–37.5	15.9	11.2	10	28.0–16.2	6.4
65A	9	10.0–23.8	16.8	4.9	2	19.7–16.2	3.2
66	36	0.7–33.4	15.0	9.6	19	33.4–11.5	4.7
67	12	8.0–30.8	18.5	7.0	2	14.1–11.8	1.8
68	14	9.3–34.6	19.8	9.9	3	34.6–24.7	4.2
69	31	18.4–37.2	29.2	5.2	20	21.3–32.9	3.7
70	30	6.7–35.2	22.1	8.7	20	12.6–31.7	8.6
71	31	4.7–35.4	20.8	8.7	20	9.3–31.8	8.2
72	16	6.6–31.0	20.4	7.9	6	14.8–22.6	3.1
73	30	7.0–36.2	25.6	9.2	21	11.3–31.8	8.9
74	15	5.2–26.0	17.8	6.1	6	13.0–19.2	2.8
75	8	5.3–29.0	15.2	6.9	3	5.3–11.9	3.7
76	5	16.2–24.9	22.5	3.2	1	24.2–24.9	0.7
C	15	1.2–18.4	9.1	4.8	1	12.2– 8.4	3.8
D	10	1.3–19.8	7.7	5.3	1	3.0– 5.5	2.5
E	10	2.1–15.2	7.3	3.7	2	8.1– 2.8	3.7
H	27	0.9–39.7	16.2	11.1	10	3.6–30.4	11.6
I	23	1.4–30.4	13.0	9.8	9	6.1–30.4	9.5
J	21	1.3–29.2	10.2	9.1	6	5.2–29.2	7.6
K	24	1.1–19.4	6.6	5.9	8	6.3–19.4	3.1
L	17	0.7–25.8	7.8	7.3	4	10.3– 6.2	1.6
M	16	0.8–31.4	9.2	8.4	4	4.5– 1.2	2.8
N	15	1.6–24.2	9.2	6.6	4	3.3– 8.3	3.3
O	15	1.9–24.8	10.6	6.5	5	2.6–10.6	4.1
P	12	1.9–26.4	12.8	7.6	4	6.0–11.5	2.3

salinity distribution for the months of February and June (Fig. 9) will show the effects of the prevailing northwesterly and southwesterly winds. The low river discharge during June is demonstrated by high salinities in East Bay and at the river mouth, but an easterly drift of low salinity water resulting from the westerly winds is obvious.

The monthly means of observed salinities, monthly estimated mean river discharge and total monthly precipitation during the sampling period are shown in Figure 10. A close negative correlation between discharge and salinity is evident, but the influence of local precipitation on mean salinity is masked by the predominant character of river discharge. This predominance is further illustrated in Figure 11. With a high rate of discharge, low salinity water, exemplified by the 5 ‰ isohaline, fills the central part of the bay as far south as St. George Island, whereas during low river stages the same isohaline is confined to East Bay and the waters near Apalachicola. Daily fluctuations in discharge rate vary from a few hundred to several thousand cubic feet per second, and such changes are rapidly reflected in the surface salinities at greater or lesser distances from the river mouth.

At Station 35 (see Fig. 1) there is an oyster bar which, except for a narrow pass of some two hundred yards, stretches from the mainland south to St. Vincent Island. The waters to the north and south of the pass are very shoal and much of the bar is exposed during the lower tide stages. This effectively serves to reduce the east-west flow of water through this portion of the bay. The flood of high salinity water from Indian Pass is restricted and this permits more complete mixing and dilution of river and high salinity water from the central bay in the region between Stations 31 and 35. It has been implied (Ingle, 1951; Ingle and Dawson, 1953) that there is a general westward flow of river water with eventual discharge through Indian Pass. This does not occur except during extended periods of easterly winds. The major outlet for the low salinity waters of Apalachicola Bay is through West Pass. Under the influence of long term or high velocity winds from the eastern or western quadrants this function of West Pass may, however, be temporarily relegated to Indian Pass or the eastern extremity of the bay. With Picoline Bar retarding water exchange through Indian Pass, the waters between Stations 31 and 35 have more stable salinities than elsewhere in the bay, and radical variations result only from excessive runoff or easterly and westerly winds of high velocity.

This interpretation is further supported by the quality of the natural oysters in this western portion of the bay. With the exception of a few small bars within Indian La-



FEB 11 - 1954
WIND SW
DISCHARGE 22361 CFS

APR 14 - 1954
WIND SE
DISCHARGE 19876 CFS

Fig. 8. a). Salinity distribution, Apalachicola Bay, under influence of southwesterly wind, February 11, 1954. b). Salinity distribution, Apalachicola Bay, under influence of southeasterly winds, April 14, 1954.

goon, there are no commercial oysters west of Station 35; whereas the largest and best quality oysters of the entire bay are to be found between Stations 31 and 35. East of Station 31 to Apalachicola and southward to West Pass commercial oysters are generally of marginal quality.

On the basis of a small number of readings, differences between surface and bottom salinities in the open bay were found to average less than 1.0 ‰. These observations indicate that there is a gradual inshore movement of more saline water along the bottom, but there is no significant vertical stratification. Short term stratification may occur during rapid fluctuations in river discharge but such gradients appear to be rapidly dissipated (It should be understood here that we are speaking in terms of estuarine gradients, which may be several parts per thousand). The shoal character of the basin and the great influence of wind on mass water movement facilitates vertical mixing and vertical homogeneity prevails in the open bay waters. Significant vertical gradients pre-

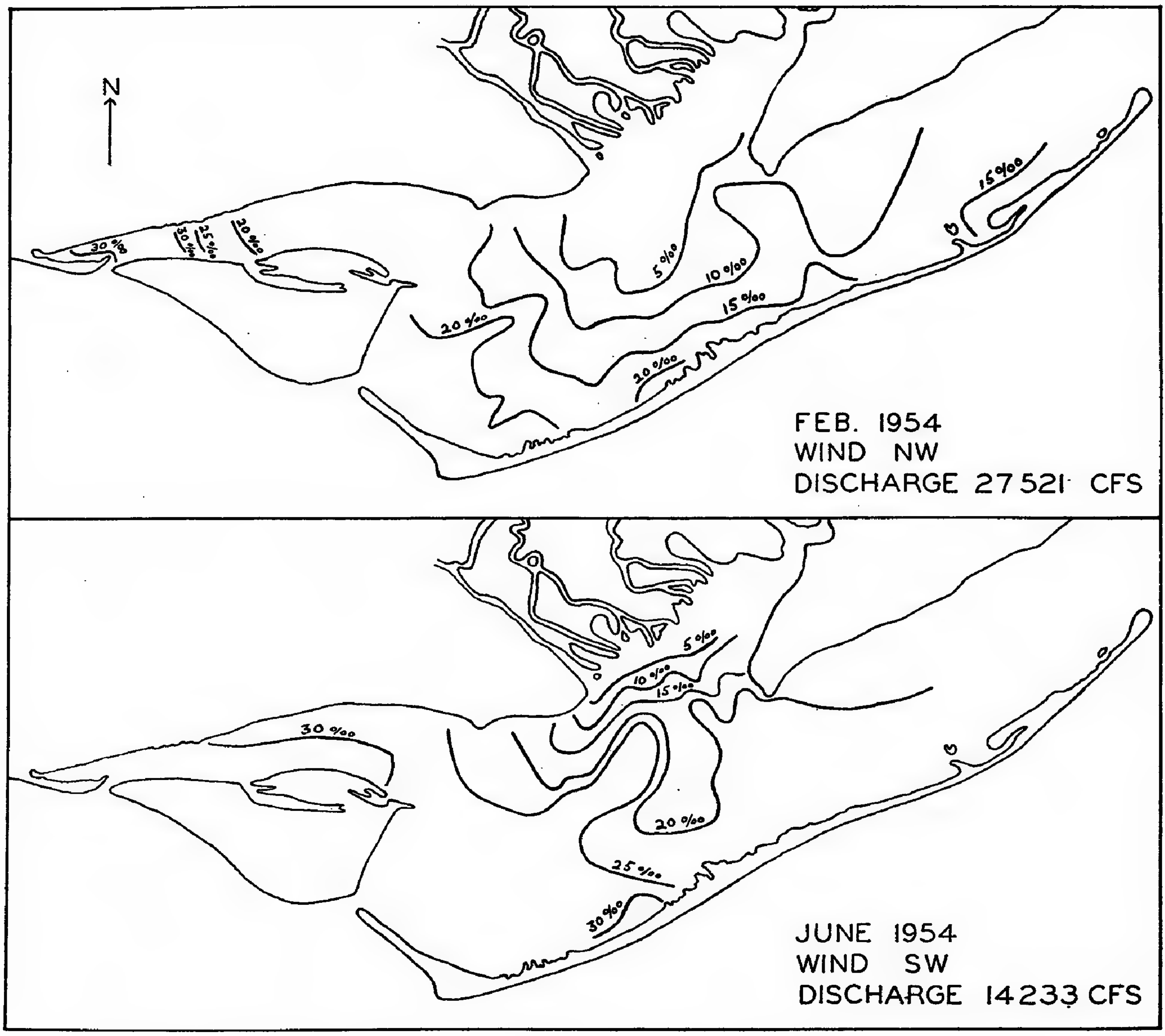


FIG. 9. a). Mean salinity distribution, Apalachicola Bay, under influence of prevailing northwesterly winds, February, 1954. b). Mean salinity distribution, Apalachicola Bay, under influence of prevailing southwesterly winds, June, 1954.

sumably occur at the river mouth and in the immediate vicinity of the passes but no supporting data are available. Even at the passes, however, high river discharge or strong northerly winds could conceivably force large quantities of mixed bay water out into the Gulf and vertical gradients would then be found in the offshore waters rather than within the bay.

There has been much speculation as to the influence that the Jim Woodruff Dam will have upon the hydrography and the oyster populations of Apalachicola Bay. While it is impossible to predict the ultimate effects of this construction, certain factors are

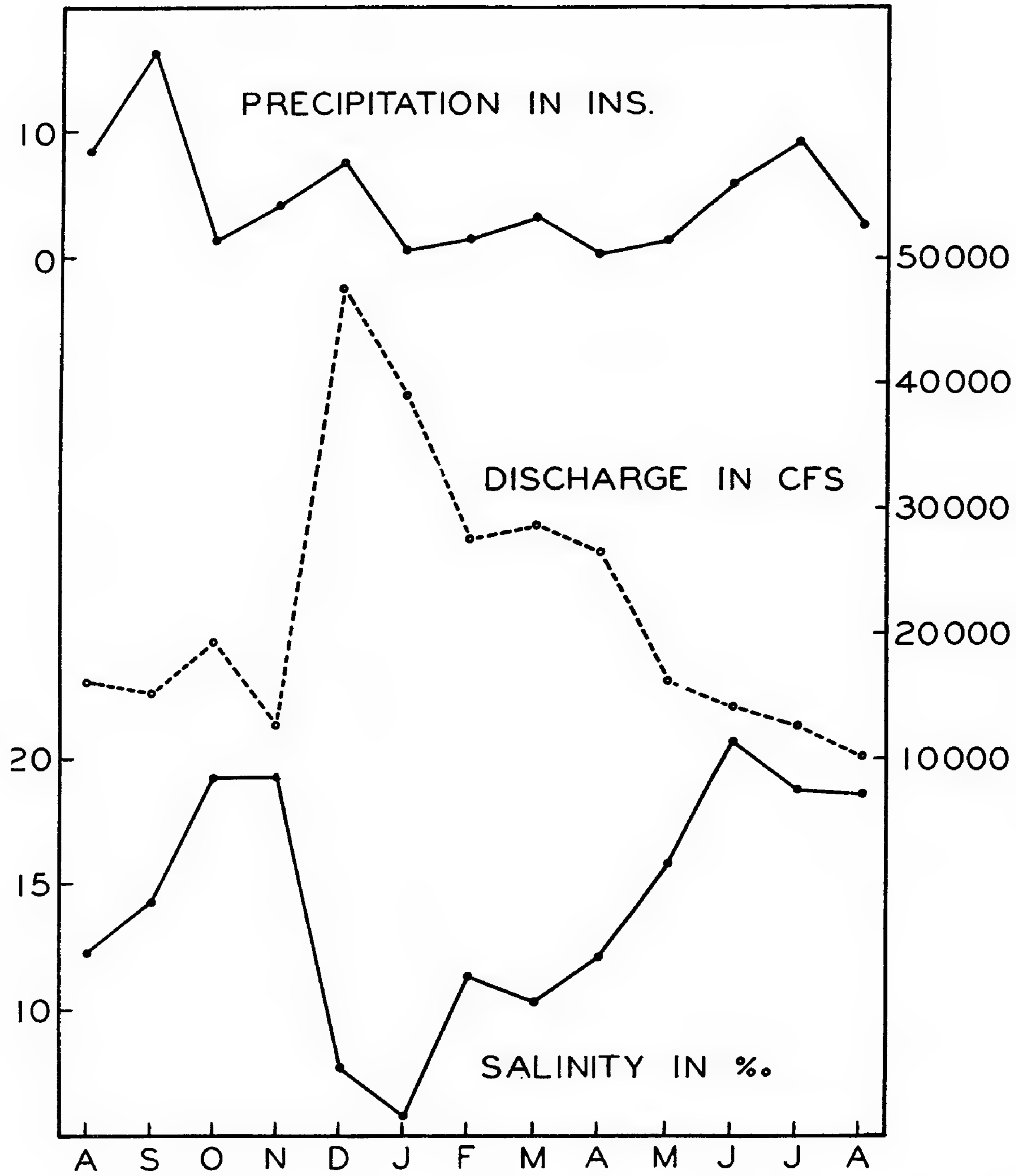


FIG. 10. Monthly means of observed surfaces salinities in Apalachicola Bay; monthly estimated mean river discharge at Apalachicola, and total monthly precipitation at Apalachicola during the period from August 1953 through August 1954.

worthy of note. It should be recognized that the Jim Woodruff Dam will have little influence on the flow of the Apalachicola River except during periods of severe drought. The dam is not primarily designed for storage purposes and, after the initial filling, reservoir level will be kept as nearly constant as possible. During periods of high discharge excess water will be released into the Apalachicola River and discharge fluctuations of the present magnitude will continue at Apalachicola. Under drought conditions navigational requirements above the dam will demand maintenance of the pool level within a one foot variation. An extreme situation is conceivable whereby there is a net water loss from the reservoir, due to evaporation, and the volume of water released is less than that entering the reservoir. Under such circumstances the dam would serve to reduce the flow of fresh water which would have been available at Apalachicola prior to its construction. With this possible exception and during the filling of the reservoir, the Jim Woodruff Dam will have little influence upon the discharge of river water into Apalachicola Bay.

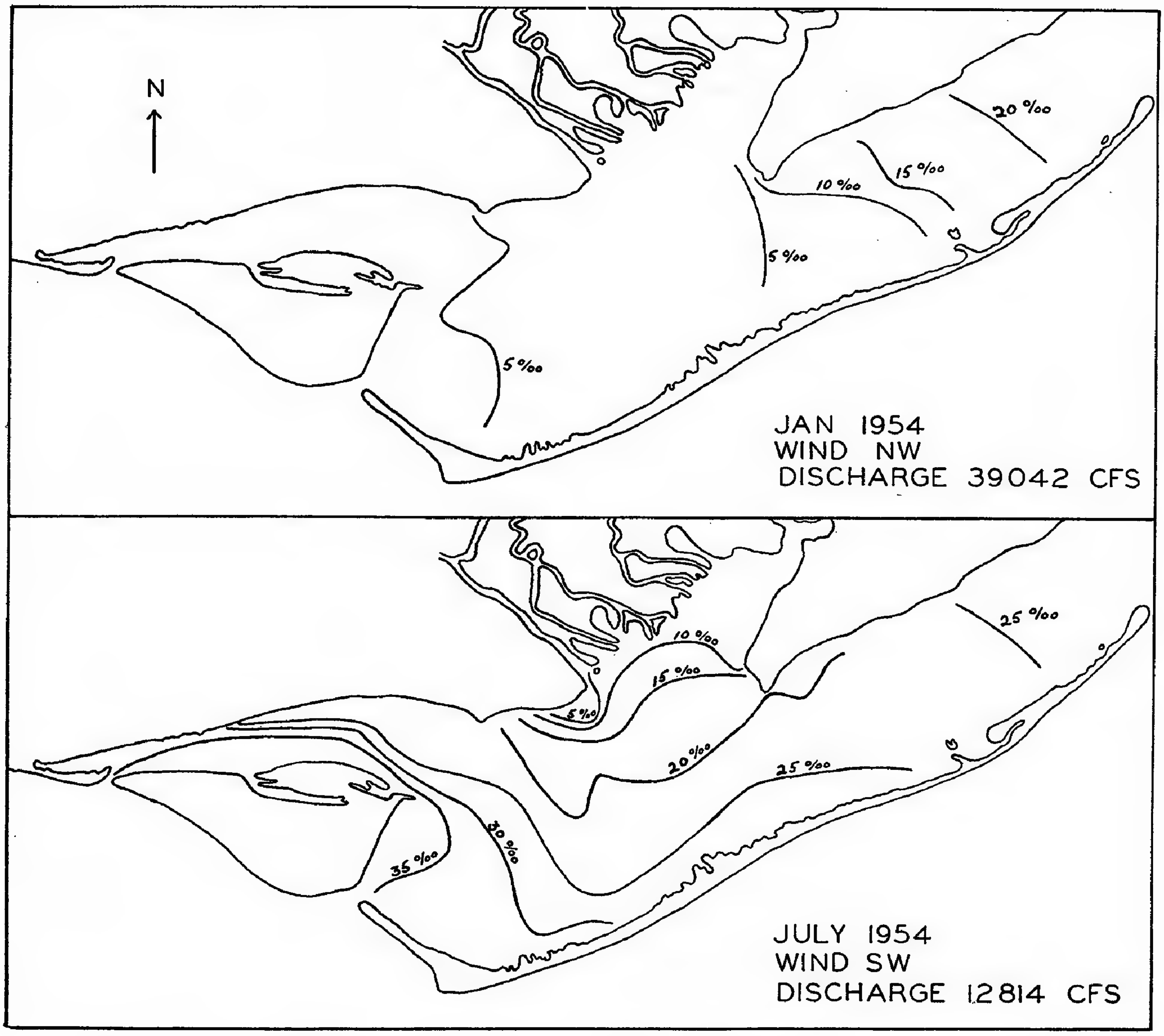


Fig. 11. a). Mean salinity distribution for January, 1954, under influence of high river discharge; northwesterly wind. b). Mean salinity distribution for July, 1954, under influence of low river discharge; southwesterly wind.

Prediction of modifications of natural conditions resulting from the maintenance of a channel through St. George Island (Fig. 1) is also difficult, but it is believed that the effects upon salinity distribution and variation will be significant in, at least, the central portion of the bay. The relatively small size of this pass is offset by high current velocity,[2] and, by its location, which reduces the minimum mixing distance between the river mouth and the Gulf by more than two miles. It can be seen therefore, that this channel will allow for diversion of much of the water which formerly flowed through West Pass, and that highly saline Gulf water will be introduced into an area which was heretofore supplied by well mixed bay waters. An immediate increase in mean salinity is to be expected in the vicinity of the pass and along St. George Island. More important however, is the fact that abrupt salinity variations, resulting from wind conditions or rapid fluctuations in river discharge, will be even more pronounced than at present in the central bay. This is based on the shortening of the effective mixing length of the basin which will permit more rapid exchange from high to low salinity than was possible through West Pass alone. To what extent the effects of this channel will be reflected in the salinity characteristics of the remainder of the basin is unknown.

Apalachicola Bay commonly experiences both long and short term salinity variations of considerable magnitude, principally caused by fluctuations in wind direction and velocity and river discharge. This condition is prominently reflected in the oyster population which varies widely in both quality and quantity throughout the area. Present salinity variations are here held responsible for the marginal condition of much of the available producing area (Ingle and Dawson. 1951). The maintenance of the new channel through St. George Island and consequent increases in mean salinities and salinity variations will doubtless be detrimental to the oyster population. Whether the commercial advantages of this channel will outweigh the probable deleterious effect upon the oyster industry cannot be here determined.

SUMMARY

Apalachicola Bay, a shallow coastal plain estuary, of the northwest coast of Florida, and the associated drainage system is discussed. The total area of the estuary is roughly 140 square miles. Apalachicola Bay is connected with the Gulf of Mexico through Indian Pass, West Pass, the eastern extremity of the bay and a recently dredged channel through St. George Island. The land drainage area which affects it directly is roughly 400 miles long and covers approximately 19,500 square miles.

The mean annual air temperature at Apalachicola is 68.7° F. with maxima during July and August and a January minimum. Total annual precipitation averages 56.29 inches and highest rainfall occurs during July, August and September.

Winds are found to be mainly easterly and northerly and those from the northerly quadrants are slightly predominant. Pronounced effects of wind on salinity distribution in Apalachicola are demonstrated. Northwesterly winds drive low salinity partially mixed river water to the eastward whereas easterly winds generate westward drift. Except under conditions of high velocity easterly or westerly winds, West Pass is the major outlet for Apalachicola Bay waters to the Gulf of Mexico.

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[2] Estimated at approximately five knots shortly after channel was completed. Personal communication from Mr. J. Martina, Jr.

Salinity characteristics are estuarine and range from nearly fresh water to 36 or more parts per thousand near the passes. Rapid short term salinity fluctuations are common throughout the area, and long term ranges of more than 35 parts per thousand are not infrequent. A close relationship was found between air and water temperatures, and a water temperature range of 25.5° C. was observed during the sampling period.

The probable effects of the dredged boat channel through St. George Island and the Jim Woodruff Dam, now nearing completion, on the normal salinity distribution of Apalachicola Bay are discussed. It is expected that the channel will result in higher than normal mean salinities in the central bay waters, and that salinity fluctuations in that area will be intensified. Except under conditions of excessive drought, the Jim Woodruff Dam will have little effect upon the normal salinity distribution in Apalachicola Bay.

REFERENCES

Austin, George B., Jr. 1954. On the circulation and tidal flushing of Mobile Bay, Alabama, Part I. Texas A&M Research Foundation, Project 24, Tech. Rept. No. 12, p. 1–28, figs. 1–18 (Processed).

(Collier, Albert). 1938. Hydrography of inland bays. Annual Report, Texas Game, Fish and Oyster Commission, 1937–38, p. 33–36, figs. 3–6.

Collier, Albert and Joel W. Hedgpeth. 1950. An introduction to the hydrography of tidal waters of Texas. Pub. Inst. Mar. Sci., (Univ. Texas) 1(2) : 125–194, figs. 1–32.

Gunter, G. 1941. Death of fishes due to cold on the Texas coast. Ecology. 22(3) : 203–208.

Gunter, G. and H. H. Hildebrand. 1951. Destruction of fishes and other organisms on the South Texas coast by the cold wave of January 28–February 3, 1951. Ecology, 32(4) : 731–736, 1 fig.

Ingle, R. M. 1951. Spawning and setting of oysters in relation to seasonal environmental changes. Bull. Mar. Sci. Gulf Caribb. 1(2) : 111–135, figs. 1–3.

Ingle, R. M. and C. E. Dawson. 1951. Variation in salinity and its relation to the Florida oyster; salinity variations in Apalachicola Bay. Proc. Gulf Caribb. Fish. Inst. 3: 35–42, figs. 1–6.

——————. 1953. A survey of Apalachicola Bay. Fla. State Brd. Conservation, Tech. Series. 10: 1–38, 1 fig.

Roelofs, E. W. and D. F. Bumpus. 1953. The hydrography of Pamlico Sound. Bull. Mar. Sci. Gulf Caribb. 3(3) : 181–205, figs. 1–11.

Storey, M. and E. W. Gudger. 1936. Mortality of fishes due to cold at Sanibel Island, Florida, 1886–1936. Ecology, 19: 10–26.

Swift, Franklin. 1897. Report of a survey of the oyster regions of St. Vincent Sound, Apalachicola Bay and St. George Sound, Fla. Rept. U. S. Comm. Fish. 22: 187–221, 1 chart.

U. C. Coast and Geodetic Survey. 1952. East Coast Tide Tables, 1954: 1949. United States Coast Pilot, Gulf Coast, Third (1949) Edition: Chart No. 1262.

U. S. Geological Survey. 1937. Drainage Basin Committee Report for the Southeastern Basins: 1954. Surface Water supply of the United States 1951. Part 2-B. South Atlantic Slope and Eastern Gulf of Mexico Basin, Ogeechee River to Pearl River. Water Supply Paper 1204.

U. S. Weather Bureau, 1953. Climatological Data, National Summary, for September: 1953–1954. Local Climatological Data, Apalachicola (Published Monthly).

Studies on Fouling Organisms of the Northwest Gulf of Mexico

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INTRODUCTION

The sessile animals and plants, commonly known as fouling organisms, which set on hard substrates have not been studied as a group in the Gulf of Mexico. These organisms are of general and theoretical interest, as well as of considerable practical concern due to increasing structural work in offshore waters by the oil industry. These structures themselves have afforded new opportunities for the setting of sessile organisms and for their study.

The work reported here was carried out on the Louisiana and Texas coasts. It was divided into two parts. The first concerned observations on oil-well platforms and the hulls of boats stationed in offshore waters. The second consisted of a study of the organisms collected on steel cylinders sunk to varying depths from two offshore platforms in Louisiana.

The first author is responsible for biological data. The second author is responsible for the hydrographic data, the photographs, arrangements for use of facilities, which were all offered by the Humble Company, and in part for the collection of samples.

OBSERVATIONAL STUDIES

The offshore platforms from which most of the observations were made are supported by a pre-welded framework of steel pipe, five-eighths of an inch thick and eight to sixteen inches in diameter. The framework of hollow tubing is lowered to the sea bottom and then made stationary by solid steel H-beams driven like piling through the tubes into the bottom. The outer surfaces of the tubing are treated with thick coatings of various asphalt base compounds and paints to keep sea water from touching the steel. These treated areas are the surfaces upon which the fouling organisms set. Figure Ia and b are photographs of templates out of the water, with fouling material attached. Figure I-c shows a close up of a template with fouling material and I-d shows templates being pulled.

A. Texas Platforms

The first platform examined was Humble E. Freeport, No. 1–278. It was located in the Gulf of Mexico almost exactly six miles from Freeport, Texas and off the mouth of the Brazos River on a course slightly south of east. The nearest land was five and one-half miles from the location in a northwesterly direction. The depth was ten fathoms. The location was completed on July 20, 1948 and the platform was pulled almost exactly a year later. It was then brought directly to shore and on July 17, 1949 Geyer took samples of the fresh fouling material and shipped them in formalin to Gunter who examined them under a dissecting microscope. The samples were taken from the waterline, thirty feet, forty feet, fifty feet, and the mudline.

The surface sample consisted mostly of a mass of filamentous, coenocytic, green alga containing hundreds of amphipods. The encrusting bryozoan, *Acanthodesia,* was present.

The main mass of the sample from thirty feet consisted of broken shells of the oyster, *Ostrea equestris,* and the barnacle, *Balanus improvisus.* Hydroids, the mud-depositing amphipod, *Corophium,* small anemones, and fungus mycelia, which penetrated the template substrate, made up the chief mass of smaller organisms present. An annelid worm and a small xanthid crab were present. Three of the *O. equestris* were 40, 52 and 55 mm. long.

At forty feet, the horse oyster, dozens of anemones, small masses of colonial hydroids and annelid worms were taken. Several small serpulid worm tubes and one slipper limpet, *Crepidula glauca,* were also taken.

The more abundant organisms, hydroids, amphipods, anemones, oysters and barnacles, were also found at the next two levels, fifty feet and the mudline. In addition, the encrusting bryozoan, *Acanthodesia,* and the small stony coral, *Astrangia astreiformis,* were found at fifty feet. Serpulid tubes were found at the bottom.

Two common oysters, *Crassostrea virginica,* were taken from depths of less than twenty feet. One was 61 mm. long and the other was 94 mm. long. These oysters were thin-shelled and had no boring clams, worms, or sponges, the perforating associates of shallow waters.

Changes of the fouling organisms with depth may be summarized briefly as follows: The waterline and subsurface was given over largely to a filamentous green alga; at all other depths hydroids, anemones, *Corophium,* and fungus were present; scattered barnacles were found at all levels, except the very surface. The oyster, *C. virginica,* was found down to twenty feet, and the flat oyster, *O. equestris,* was found from about twenty feet to the bottom. Encrusting bryozoans, *Acanthodesia,* were rather widely scattered, but were found from the surface to fifty feet. Serpulid tubes were found from forty feet to bottom. Crepidula was also found at forty feet and the coral, *Astrangia,* was found at fifty feet, but neither was found on the bottom.

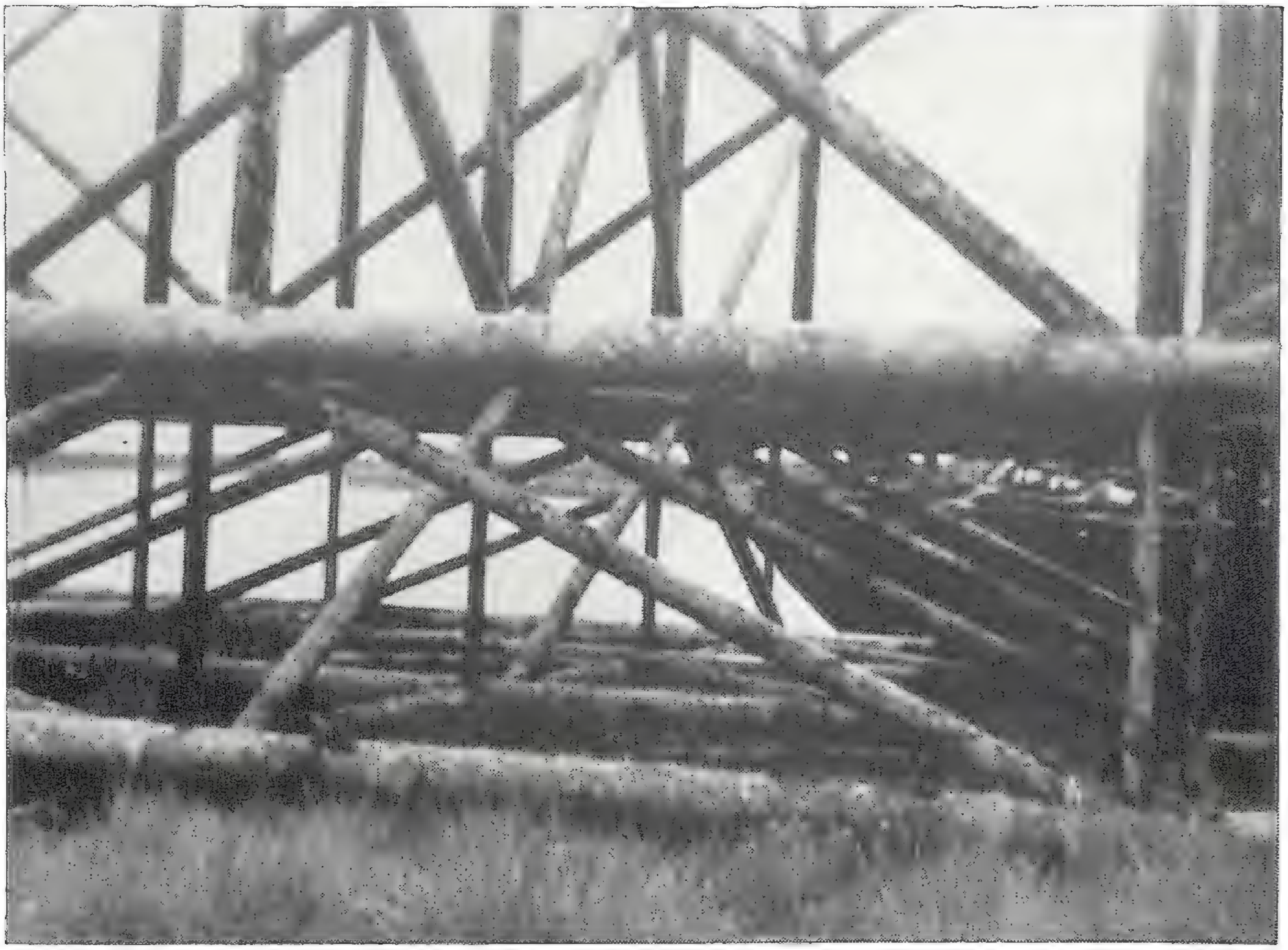
The second platform examined was Ohio Melben & Humble No. 1–248. It was located ten and a half miles ENE of Freeport and four miles off the Gulf beach just south of Oyster Bay. The bottom was mud and the depth was fifty-two feet. The structure was coated with red anti-fouling paint and was put down on July 1–9, 1948. It was pulled on July 5–15, 1949, thus having been in the water almost exactly one year. It was examined on July 16 as soon as it was brought to shore.

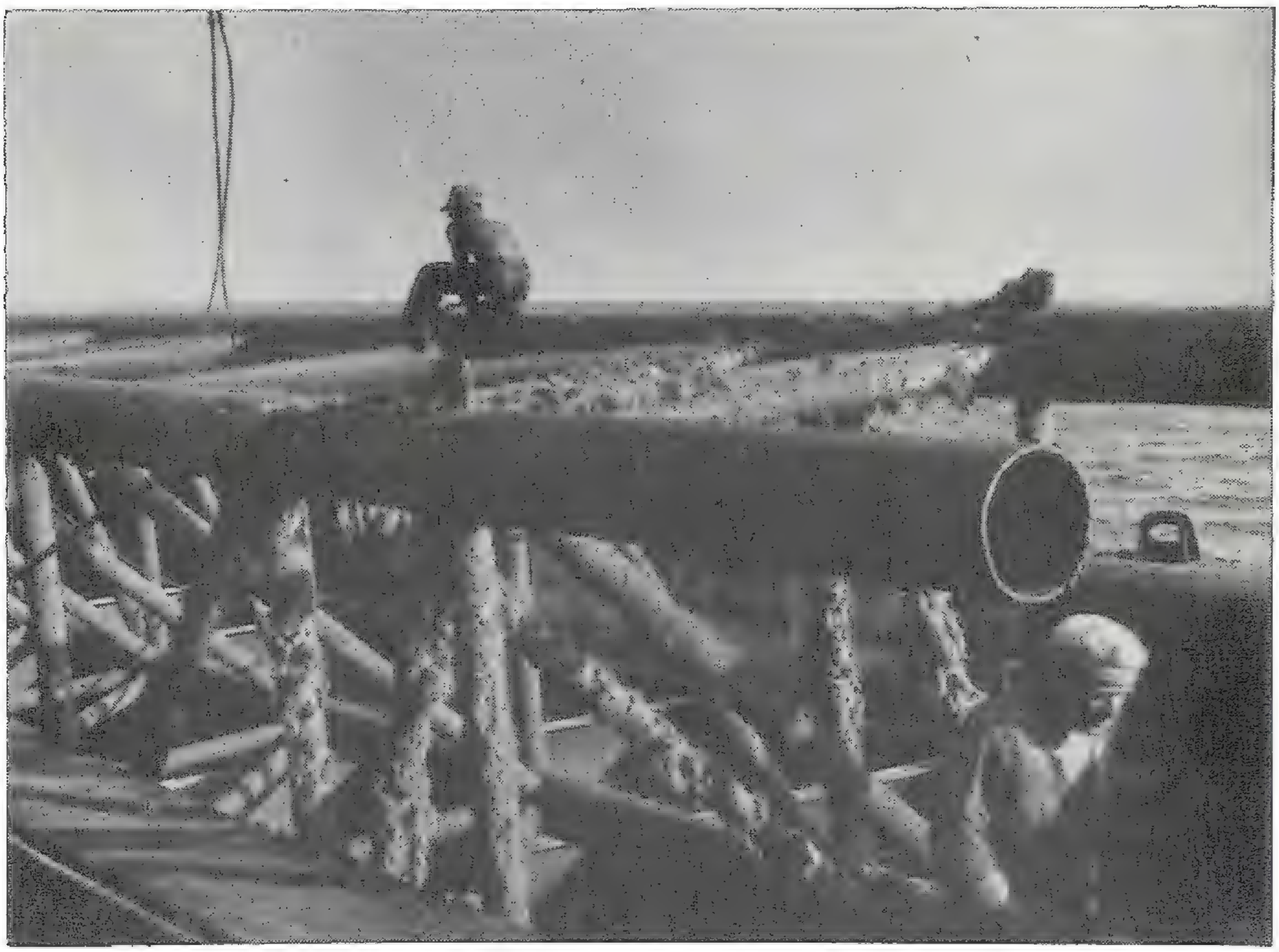
A small block of wood had been wired to the bottom of one template. It had been so honey-combed with teredos that it was soft and could be pressed with the hands like heavy cardboard. The teredos had eaten all the wood, leaving only enough to form a thin partition between their own chambers.

Since the organisms were partially dried out, amphipods, small anemones and other small fragile organisms were not noted, although they were undoubtedly present.

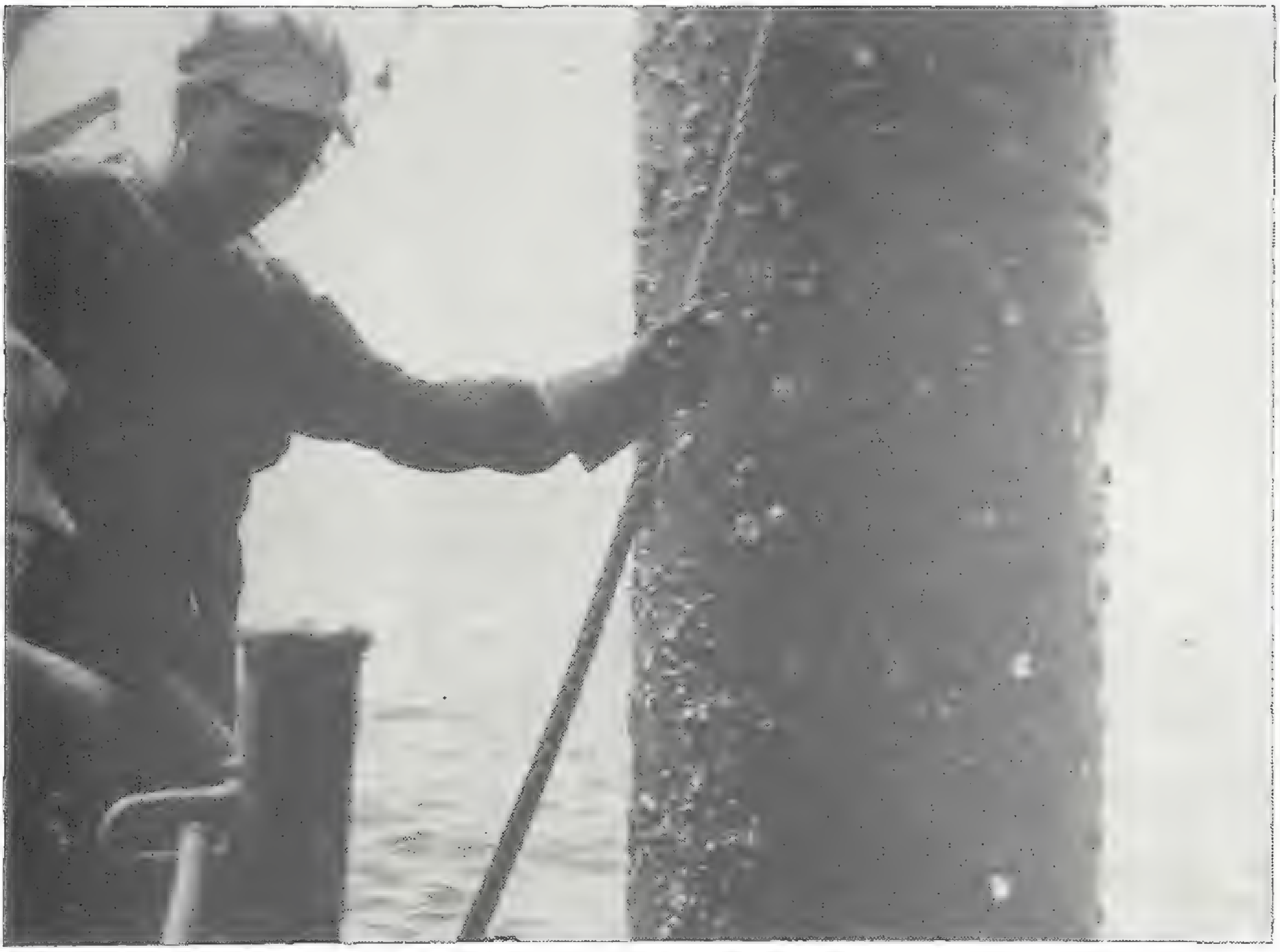
At the bases of the templates, right at the mudline, there were large masses of an unidentified colonial hydroid a foot in length. The holdfasts were intermingled with a crust of bryozoa. A few barnacles and small pinnid shells, probably *Atrina,* were found among the hydroids. This material extended to the first cross-piece, two feet or so from the bottom. At the level of the cross-piece there were a few serpulid worm tubes, some small barnacles, one cm. across, several flat oysters, *Ostrea equestris,* up to four cm. long, and several slipper shells, *Crepidula.* Everything was covered with a crust of the bryozoa, *Acanthodesia.*

At the second cross-piece, about eighteen feet from the bottom, the oyster, *O. equestris,* up to 28 mm. long, was abundant. Two species of barnacles, *Balanus improvisus* and *B. amphitrite,* were present. The whole was covered with the encrusting bryozoan.





Figs. Ia and b. Two views of templates out of the water with fouling material attached.



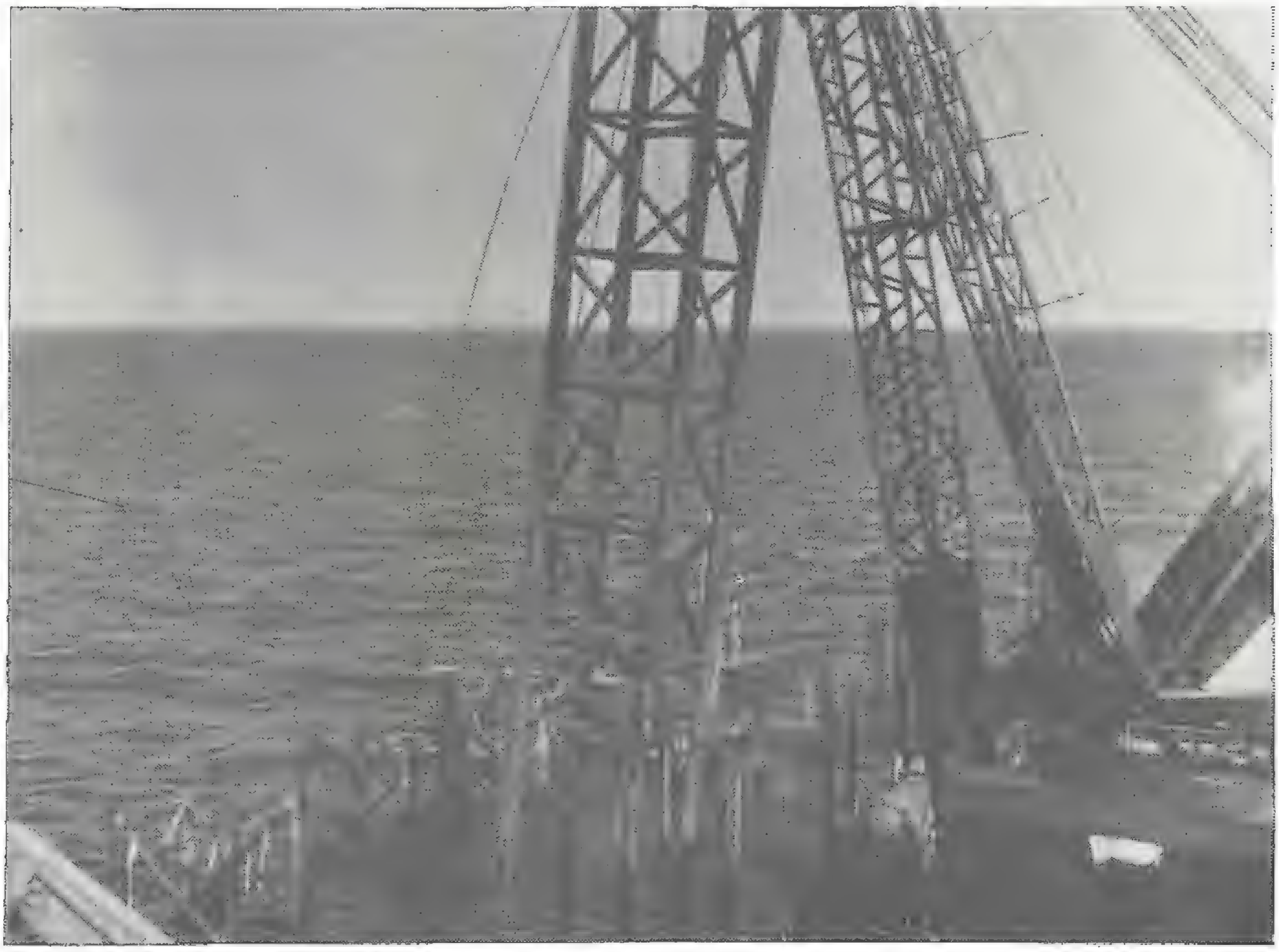


FIG. Ic (top). A close-up of a template showing fouling material attached.
FIG. Id. A picture of templates being pulled.

At the third section, approximately 27 to 40 feet from the bottom, the only large organisms present were the oysters, *O. equestris* from 5 to 45 mm. across, and the two species of barnacles up to 50 mm. across. One *Crepidula* was found. The whole was encrusted with bryozoa. The oysters were in spawning condition.

At the fourth cross-piece, about twelve feet from the surface, *O. equestris* 37 mm. long, with ripe gonads, were present. Five small pelecypods, *Arca,* were found. A few pinnids, ranging from 33 to 52 mm. long, were also taken. There were a few hydroids and much less bryozoa at this level. Only one species of barnacle, *B. improvisus,* was taken at this level. The individuals were all around 18 mm. in diameter. Several commercial oysters, *Crassostrea virginica,* were also taken. They ranged from 45 to 80 mm. in length, the latter being close to the market size of 3.5 inches. A few small spat 7 to 8 mm. long were attached to the large oysters. The small spat were only a few weeks old and the larger oysters were almost a year old. Evidently the spat struck at this location two years in succession. The same thing may be said of the barnacles. On the first and second sections, 0 to 25 feet from the bottom, the barnacles were small, being around 18 mm. long, and were very thick. On the upper half of the templates the barnacles were fewer and much larger, ranging up to 5 cm. across. Evidently, barnacle larvae set at the upper levels in 1948 but set much more abundantly on the lower half of the templates in 1949.

In summary: Small barnacles, *Ostrea equestris,* and a bryozoan dominated the fouling organisms on the lower twenty-five feet of the templates. They were very thick and coated the column. On the upper half these organisms became much thinner and near the surface a few commercial oysters, *C. virginica,* were present. A mass of hydroids were the dominant sessile organisms at the mudline. *Arca, Crepidula* and pinnids were only incidental and mostly at lower levels.

B. Louisiana Platforms

A platform in the Gulf seven miles SE of Quatre Bayou Pass, Louisiana was started on October 18 and completed November 27, 1948. The depth was thirty-eight feet. It was dismantled on June 30–July 4, 1949. Samples of the dried fouling organisms were scraped off by Geyer three days later and sent to Gunter for examination. It is seen from the above dates that the organisms grew in a period of seven and one-half months.

The fouling assemblage as shown by the dried samples was very simple, consisting of four animals and one plant. The samples were made up chiefly of broken barnacle shells, *Balanus eburneus,* and the encrusting bryozoan, *Acanthodesia,* in much smaller mass. The abundance of barnacles increased from the surface to the twenty foot level, and declined from there to the bottom where they were scarcer and smaller. Some of the barnacles grew 35 mm. (1.4 inches) in approximately seven months. The smaller sizes were about 8 mm. across. The bryozoan was least abundant at the surface and in greatest abundance at the thirty foot level. It was sparse near the bottom. At the surface the barnacles and the bryozoan were overgrown with a mat of filamentous alga, which was found at no other level. One small *Arca* was found at the surface and an oyster borer, *Thais haemostoma,* 37 mm. long, was found at the thirty foot level. No oysters were present.

The second Louisiana platform examined was an Humble location known as Platform B of Block 30, West Delta. It was fifteen miles SE of Barataria Pass and fifteen miles NW of Southwest Pass of the Mississippi River. The depth was fifty feet. This platform was completed April 5, 1949 and was pulled February 12, 1950, having been in the water a little over ten months. The fouling organisms were examined on February 15.

On this platform magnesium strips had been placed in the water at a minimum distance of five feet from the templates and connected to them with a copper wire. This system acted as a battery with the magnesium being the anode and the templates the cathode. It is effective in impeding corrosion of the metal. Such systems are designed to draw from 5–10 milliamperes/ft.^{2} of steel at less than one volt. The system did not prevent fouling.

Within a foot of the surface there was a thick beard of filamentous green alga. There was heavy fouling on the upper sixteen feet of the templates. The surface was crusted with *Acanthodesia* and hydroids. A few anemones were present and thousands of small amphipods were present. A few small *Arca* and some annelid worms were present. One small stone crab, *Menippe mercenaria,* was seen. A superficial glance at this level would indicate that the bryozoan and barnacles were practically the only organisms present. One group of barnacles, not numerous but scattered at all depths, was 3.2–3.8 cm. across. It was *Balanus eburneus.* Some contained ripe eggs. It is interesting to note that the average minimum growth rate of the larger specimens was 0.13 mm. a day. A second group of the same species was 1.9–2.5 cm. across. They were also scattered. A second species, *B. improvisus,* around 1–3 cm. across, was very abundant at this level and was the most striking component of the fouling. It was scattered or absent at lower levels. Closer examination showed that small barnacles 2 mm. across were present. The species was not determined. Ten *Crassostrea virginica,* 4.7 to 9.2 cm. long, were taken at this level. The average length was 8.1 cm. The minimum growth rate of the largest oyster was 0.3 mm. a day.

The next zone down extended from sixteen to thirty-seven feet. Compared to the top and bottom zones, it was relatively barren. The surface was fairly thickly covered, however, with almost invisible hydroids about 0.5 cm. high. A few small patches of the stony coral, *Astrangia astreiformis,* were present. There were a few *Acanthodesia* patches and some calcareous worm tubes. Large barnacles, *B. eburneus* with ripe eggs were scattered over this zone. There was also a scattering of *B. improvisus* around 2 cm. across. Scattered specimens of two oysters, *Ostrea equestris,* and the tree oyster, *Ostrea frons,* were also found at this level. The maximum size of the former was 7.2 cm. in length and *frons* ranged from 3.8 to 5.1 cm. long. This is the first discovery of the tree oyster on the northern Gulf Coast and a previous account was given by Gunter (1951).

The transition between the top, midlevel, and bottom zones took place within a foot, and the paucity of sessile animals on the midzone was striking. The reason for this comparative scarcity on the midzone is unknown, but it may be significant that very little of the covering compound was present along the templates at this depth and scrapings gave a thin layer of the compound and considerable rust. Thick layers of the compound and no rust was found at the other two levels. It may be that the anti-cathodic protection, described above, had some anti-fouling effect where the covering compound was thin and the organisms were not well insulated from the underlying steel.

The lower thirteen feet of the templates comprised the third zone. It was fairly extensively covered and in some places matted with tubes of serpulid worms. Large patches of *Acanthodesia* covered these tubes and a second species, *Membranipora*, was present in lesser abundance. A few patches of the coral, *Astrangia*, and a few of the large *Balanus eburneus* were present at this level.

In summary: A beard of filamentous green alga was found at the very surface. The upper sixteen feet was encrusted with *Acanthodesia* and hydroids. A barnacle, *B. improvisus* was also abundant at this level and a few common oysters, *C. virginica*, were found. At sixteen to thirty-seven feet a few patches of *Astrangia*, scattered barnacles, *B. improvisus* and *B. eburneus*, and scattered specimens of *Ostrea equestris* and *O. frons* were found. This section was relatively barren. The lower section, thirty-seven to fifty feet in depth, had large patches of two encrusting bryozoans, mats of worm tubes and a few patches of *Astrangia*. A few large *B. eburneus* were present at all three levels.

C. Discussion

Several factors effect the fouling communities described here. Among the more obvious ones are light, turbidity and salinity. These all vary with depth.

Figures II and III are schematized diagrams of depth distributions of organisms on the platforms at the two localities, which may be described roughly as off the Brazos River and west of the Mississippi River mouth. They show several things in common, along with certain inexplicable differences. Hydroids, *Corophium* and *Acanthodesia* were present at all levels at both locations. The arc shells, *Arca transversa*, and filamentous green alga were found at the upper levels at both localities. Similarly, serpulid worm tubes and the coral, *Astrangia*, were found at lower levels only. *Crepidula* and *Atrina* shells were absent from the Louisiana platforms, but small ones could have been overlooked.

The common Virginia oyster, *Crassostrea virginica*, could not have been easily overlooked, and it was absent from the inshore Louisiana platform lying offshore from some of the largest oyster beds in the world. In contrast, this oyster was found on both Texas platforms, which lay off the mainland and some distance from one small bay with no oyster production of a commercial scale. The only other place on this coast where the common oyster grows outside of the bays is off the mouth of the Atchafalaya River, where several natural reefs were reported by Cary (1906), who gave a map of these beds. The beds are still there and Hedgpeth (1953, p. 151) republished the figure, which is a fairly accurate representation of the situation today except for minor details.[1] *Crassostrea virginica* is a common estuarine species and the fact that it would grow five miles offshore on the Texas coast did not come to light until these platforms were put up. Apparently the oysters grow only at upper levels where the salinity is low, and the platforms are the first hard substrate they have had available at these levels. This point is of interest from the standpoint of oyster biology, for it suggests that wastage of far drifting oyster larvae may be considerable over the vast expanses of the Gulf. The rapidity of growth of these common oysters, in the absence of their usual shell-boring associates (the boring sponge, *Clione,* the boring clam, *Martesia,* and the mud-worm, *Polydora)* has been mentioned before (Gunter, 1951). The fastest minimum growth rate was 0.3 mm. a day.

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[1] Mr. C. E. Dawson has informed us that oyster reefs exist in several places off the west Florida coast in the open Gulf out to five miles offshore. This interesting situation has never been studied or described. Price (1954) has mentioned this fact.

The horse oyster, *Ostrea equestris* was found at both localities, at lower levels. The tree oyster, *Ostrea frons,* was found only in Louisiana.

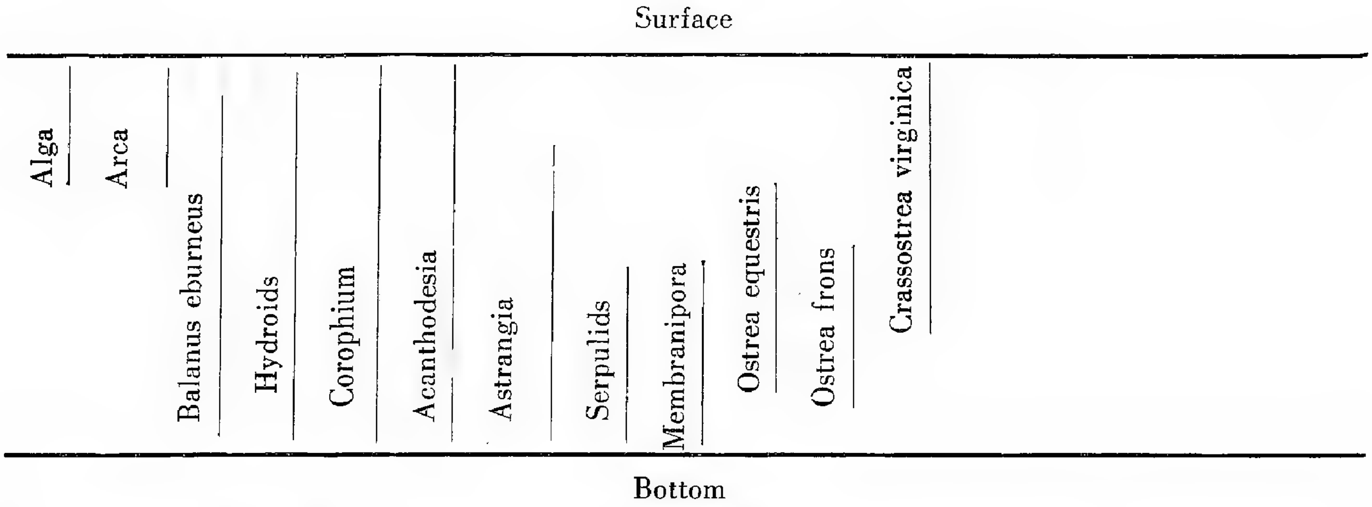

Surface
Alga
Arca
Balanus eburneus
Hydroids
Corophium
Acanthodesia
Astrangia
Serpulids
Membranipora
Ostrea equestris
Ostrea frons
Crassostrea virginica
Bottom

FIGURE II. A schematized distribution of the fouling organisms along the two Louisiana oil-well platforms described in the text. The greatest depth was fifty feet.

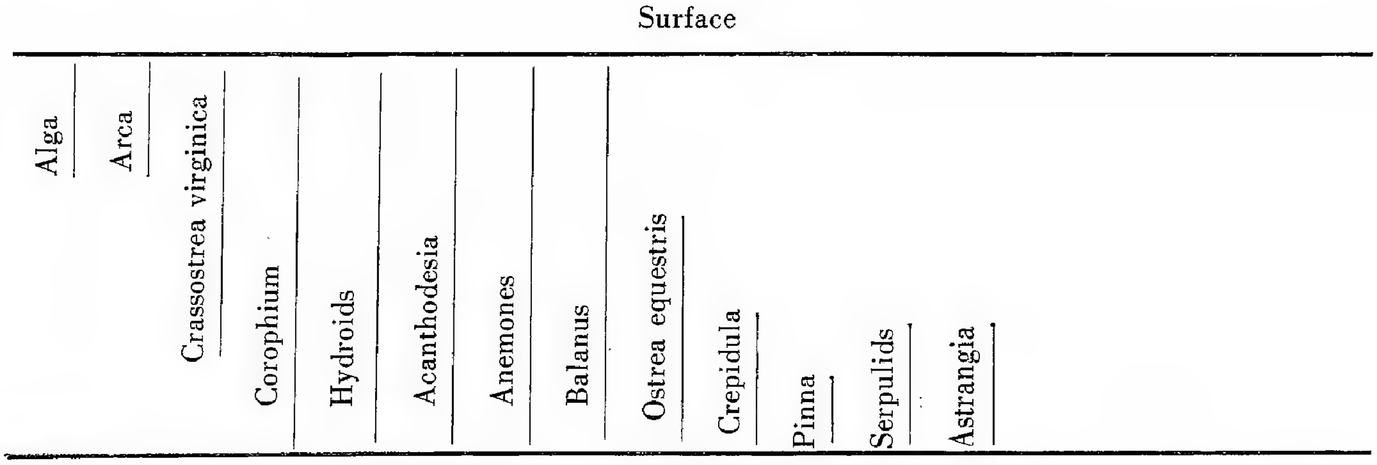

Surface
Alga
Arca
Crassostrea virginica
Corophium
Hydroids
Acanthodesia
Anemones
Balanus
Ostrea equestris
Crepidula
Pinna
Serpulids
Astrangia

FIGURE III. A generalized graphic distribution of the common fouling organisms along the two Texas oil-well platforms described in the text. The greatest depth was sixty feet. Except for the alga, organisms were not found right at the surface or right at the mudline. Relative abundance at depths are shown very roughly by thickness of the lines.

D. Fouling Organisms on ST-7

This boat was brought to the Alabama Dry Dock in Mobile where Gunter examined it on October 23, 1950. It had been in water seventeen months, being stationed from May to November, 1949 at the Tiger Pass area and from December to September in the South Pelto area of the Louisiana coast. These are both in the open Gulf of Mexico. The first is approximately five miles west of Tiger Pass of the Mississippi and the second is fifteen miles south of Terrebonne Bay. A summary of salinity readings at these two locations are given in Table 1.

The fouling complex was very simple. At the surface and along the upper one and a half feet, just below the water-line, there was a growth of filamentous green algae thick enough in spots to hang down as a thin beard. No other sessile organisms were present in this part of the hull, with the exception of a few scattered goose barnacles. Mostly these were a little below the surface but in some places extended up to the waterline. They were not very numerous but were scattered and extended down to the second lap of the plates above the bilge. Their abundance was one to a square foot or less. This species, *Lepas pectinata,* prefers a higher salinity than the acorn barnacles and it is somewhat peculiar that the larger growth of acorn barnacles was on the lower parts of the boat, while the more saliniphilous *Lepas* was at the surface where water of lowest salinity would be expected. It is possible that light also has an effect on the setting of *Lepas* so that it will not grow much below the surface in turbid waters.

TABLE 1.

Summary of Salinity Readings at Anchorage of ST-7

Tiger Pass, 1949

Months	June	July	August	September	October
Number	15	14	22	11	15
Average	27.8	23.6	25.5	26.1	29.5

South Pelto, 1950

Months	January	February	March	April	May	June
Number	6	15	19	5	10	12
Average	26.2	30.4	31.6	31.0	32.1	30.7

Between the first and second laps of the plates there were a few scattered oysters and a few scattered acorn barnacles about 12 mm. in diameter. The whole surface was covered with a short fuzz of colonial hydroids. Below the first lap of the plates, which was practically at the lowest part of the sides where the bottom began, the whole area was covered with the small acorn barnacles, *B. improvisus,* almost but not quite as thick as they could stick along the bottom. They were 8 to 12 mm. across. The free space was covered with the above mentioned hydroids and literally millions of small anemones approximately 3 mm. across. These anemones and the small barnacles were not particularly conspicuous but they formed a large part of the fouling. The great majority of these barnacles were dead and live ones were rare. More conspicuous were three other organisms, one a large cone-like barnacle, *B. tintinnabulum,* up to 85 mm. (3⅓ in.) in diameter. It was scattered, with one to every hundred square feet. In spite of its conspicuousness, the barnacle was really a rather insignificant part of the fouling assemblage. This is the only time this species was encountered during this investigation, in conformity with the statement of Redfield and Deevy (1952, p. 40) that some varieties of this species have been found only on ships. Still more abundant were the oysters, *Crassostrea virginica,* most of them being between two and three inches long. On the bottom of the boat oysters were present at the abundance of about 12 to 36 per square yard, or somewhat in excess of 100 barrels to an acre. On the sides, between the laps of the plates, there was approximately one oyster to the square yard. The hull of the boat had the appearance of a thinly scattered reef and there were several barrels of oysters on it. Mudworms, boring clams and boring sponges were absent. The oysters themselves were not quite up to market size. Scattered among the oysters and much thinner in population was the jingle shell, *Avicula.*

The inside of dead oyster shells was often found to be inhabited by baby stone crabs, *Menippe mercenaria,* and the small blenny, *Hypsoblennius ionthas.* On the stern of the boat and along the rudder there were a few patches of the bryozoan, *Acanthodesia.* One oyster borer, *Thais,* was found on the hull.

In summary: Under the hull the chief living sessile organisms were the common oyster, the large barnacle, *Balanus tintinnabulum,* the scattered jingles, *Avicula,* and millions of small anemones, plus a fuzz of colonial hydroids which covered almost everything except the anemones. The appearance of a host of small barnacles, *B. improvisus,* was deceiving. Only dead shells of these remained for the most part.

1. THE SEA-CHESTS

Two ballast tanks and two of the sea-chests within the ballast tanks of this boat were examined. The starboard aft sea-chest was open to the water but the ballast tank had not been used. On the inside of the chest, near the ½-inch holes through the hull plate, there was one small patch of barnacles of ½-inch size. There was a scattering of large oysters in the chest up to 3 inches in length. The holes through the hull plate were somewhat occluded by fouling organisms growing on the outside, although there was little growing on the inside and nothing was growing on the screen inside the chest to impede water flow. The walls of the chest were covered with a thin growth of bryozoa. The growth of *Acanthodesia* within the chest was in contrast with what was found on the outside. Apparently the hydroids and other organisms outgrew the bryozoa so much on the outside that it was smothered out. No hydroids grew in the chest.

The starboard forward chest contained several large oysters scattered about on its walls. The lengths of three of them were 4⅜ inches, 3⅝ inches, and 3½ inches. Several dead oyster shells were on the bottom of the chest and three *Thais* were taken out of this chest. They were 2½ to 3 inches long and 1⅜ inches in diameter. Several baby stone crabs were on the floor of the chest and there was one large stone crab present. It had a carapace width of approximately 3½ inches and was about as large as a man's fist. A white trout *(Cynoscion)* 6 inches long was also present in the chest and there were about a dozen *Hypsoblennius.* There were a few scattered barnacles in this chest and all of the inside was covered with the bryozoan, *Acanthodesia.* There were also a few small patches of the coral, *Astrangia.* The coral was alive and seemed to be in good condition.

The walls of the ballast tanks were covered with thin layers of rust and nothing else. Organisms were not seen.

Several of the animals taken in the sea-chest were much too large to get out through the holes of the plate. They evidently grew up within the chest and maintained themselves as a more or less isolated community.

2. SUMMARY

In general, with the exception of *Lepas,* the fouling along the bottom and within the sea-chests of this boat suggested a highly saline, estuarine environment rather than that of the open sea. The *Thais,* common oyster, bryozoans, acorn barnacles, and even the coral, *Astrangia,* are found in the more saline parts of estuaries.

The absence of the boring sponges, boring clams and mudworms from these oysters was the same as noted before on oysters from the platform templates. Since the fouling on this boat was characteristic of the saline estuary and since the boat had doubtless been exposed to fairly low salinities at times, there was no known reason why mudworms and boring clams were not present. Their absence was something of a puzzle.

FOULING COLLECTOR STUDIES

A. Introduction

Two offshore drilling platforms of the Humble Oil & Refining Company in Louisiana waters were used as locations for this study. The first is known as Grand Isle A and lies five miles SSE of Barataria Pass. The second, known as Caminada A, lies four miles SSE of Caminada Pass. These two passes are at the east and west ends, respectively, of Grand Isle. A photograph of Grand Isle A is shown in Figure IVa. A view underneath the platform is shown in Figure IVb. The area lies thirty miles northwest of Southwest Pass of the Mississippi River.

B. Methods and Plan of Work

The fouling collectors used were cylinders of steel pipe, eight inches in diameter with an outside surface area of one square foot. These were strung on steel cables about fifteen feet apart. The top cylinder was suspended at two feet below mean Gulf level and the lowermost one was about two feet above the bottom. Two links of heavy chain, weighing about thirty pounds, were suspended on the lower end to keep the cylinders from being tossed about by the force of the seas. Figure V is a diagrammatic drawing of the apparatus.

In addition to the cylindrical collectors, two flat plates one foot square were suspended about four feet under the water. These were also weighted by chain links, but the whole ensemble swung free in the water and no part touched bottom.

The original plan was to put two sets of cylindrical collectors and one flat plate on each platform. One set of the cylinders and the flat plate were to be changed every three months and the other set of cylinders was to be left in the water a year. As is usual in such cases, the plan was only approximated. The changes were made at three and a half to six month intervals over fourteen months and the unchanged set was left in the water for fourteen months. The first flat plates were only put down at the time of the first exchange, four months later than the first cylinders. The tables show the dates at which the collectors were put down and taken up, except for the first time. These were placed at Grande Isle A on November 27, 1950 and at Caminada on December 15, 1950.

C. Observations and Results

1. HYDROGRAPHIC DATA

The water depth at the two locations is approximately 50 feet. Salinity data are not available for the period of the fouling tests for the Caminada Pass area. However, a detailed discussion of these conditions for the period January through September 1949, has been published (Geyer, 1950). The average salinity at this location was 30.1 ‰ and the values range from 15 to 36 ‰. There is no reason to believe that salinity conditions vary appreciably from these values during the fouling test period.

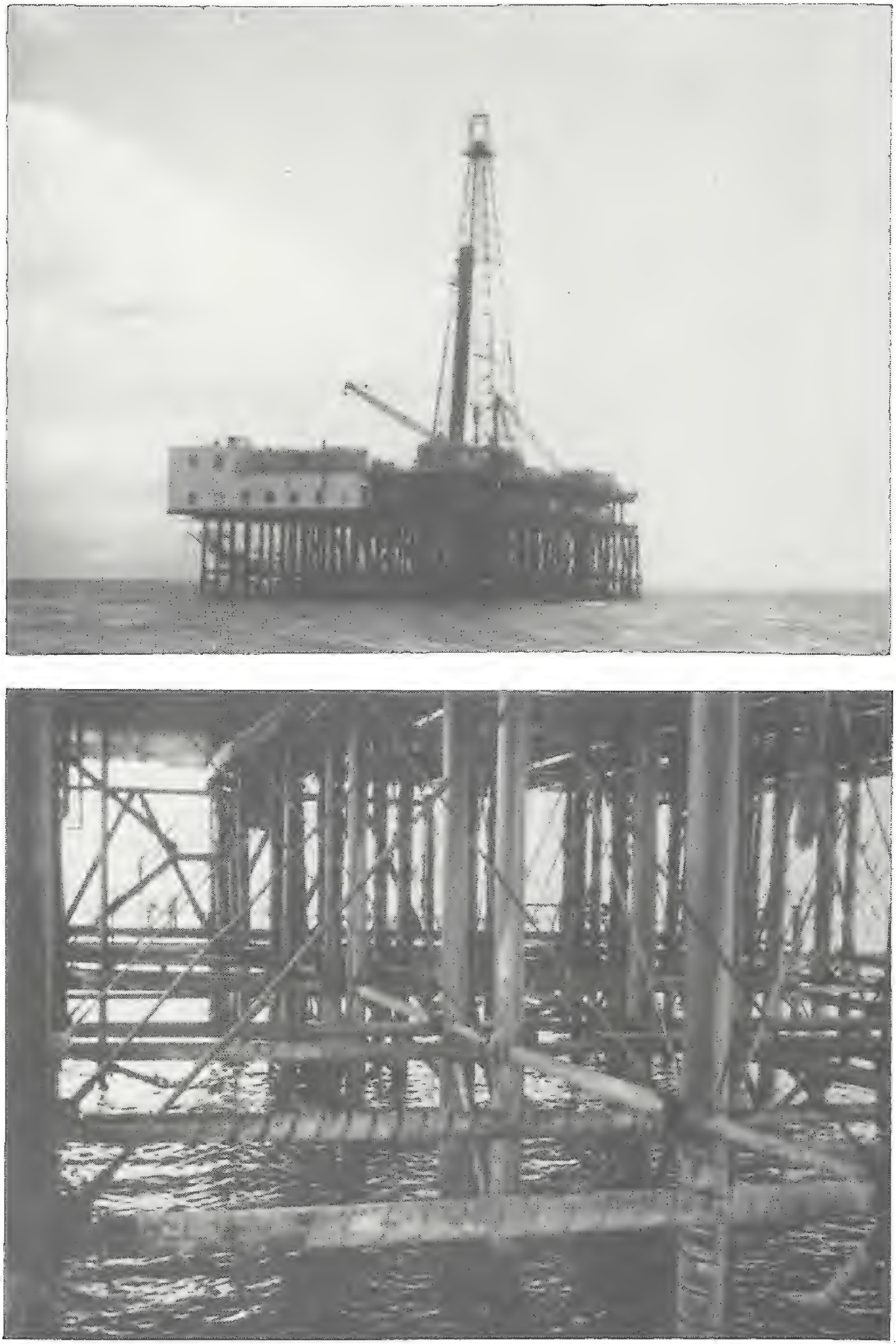


Fig. IVa and b. A photograph of the Humble platform Grand Isle A and a view underneath the platform.

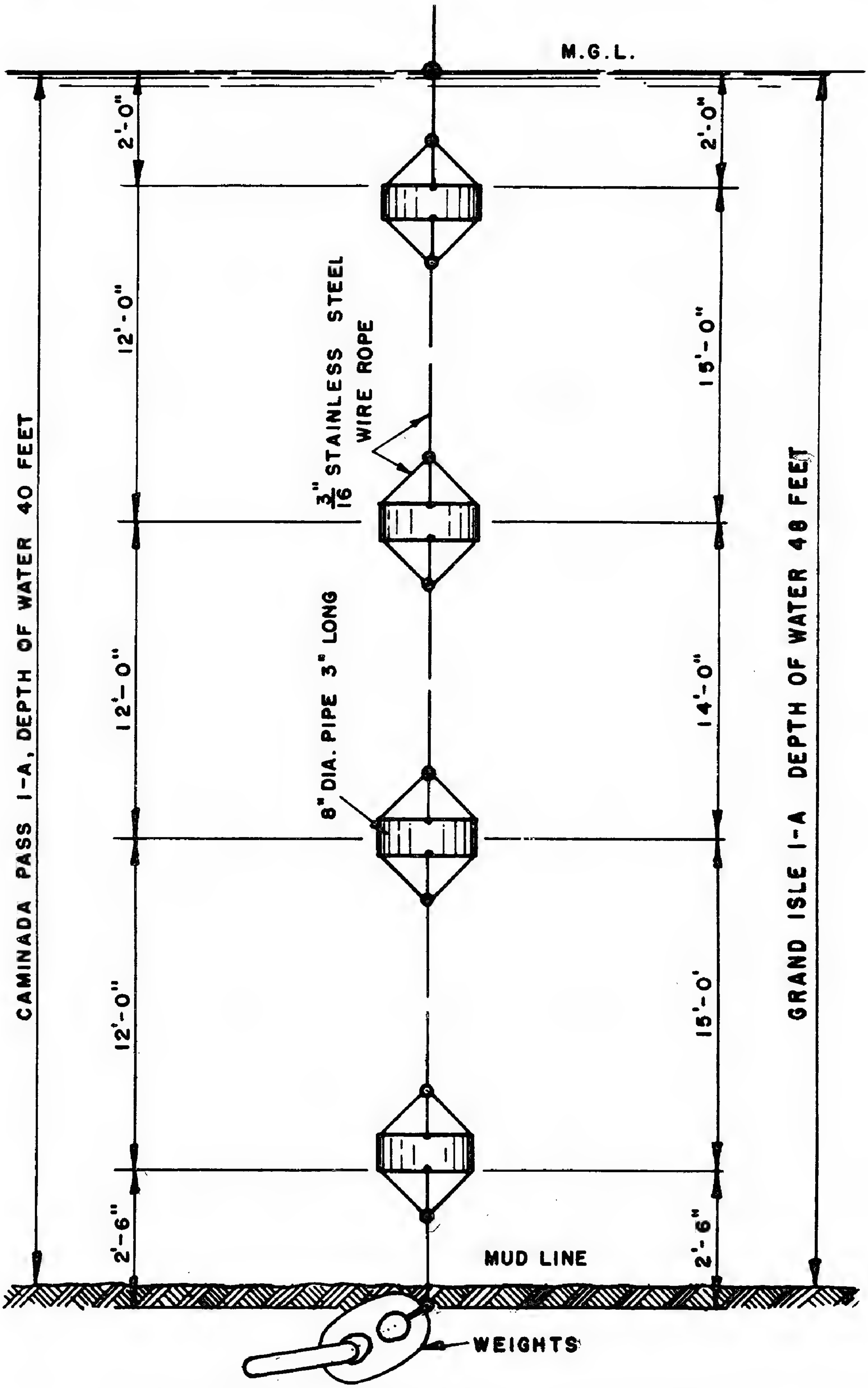

M.G.L.
CAMINADA PASS I-A, DEPTH OF WATER 40 FEET
2'-0"
12'-0"
12'-0"
12'-0"
2'-6"
$\frac{3}{16}$" STAINLESS STEEL WIRE ROPE
8" DIA. PIPE 3" LONG
2'-0"
15'-0"
14'-0"
15'-0'
2'-6"
GRAND ISLE I-A DEPTH OF WATER 48 FEET
MUD LINE
WEIGHTS

FIG. V. A diagrammatic drawing of the fouling collectors in place.

Almost daily salinity observations, together with air and water temperatures were available at the Grand Isle location, beginning in January of 1951, only about a month after the initiation of the fouling study began. The monthly range in salinity observations at the Grand Isle "A" platform for the period 1949–53, is shown in Figure VI. In addition, a comparison of the range in salinity for each of the two years is shown. The monthly extreme range in salinity, namely from 10 to 36 ‰ which occurred in March 1951, is essentially the same as that for the period January through October 1949 (Geyer, 1950). The effect of the variation in discharge of the Mississippi River on the salinity characteristics of offshore areas is demonstrated again in an analysis of these data. For example, maximum salinity and minimum variation in salinity occur during the late summer and early fall months of the year. The minimum variation in salinity occurred in November 1952, when the salinity varied only 4‰ for a minimum of 30 and a maximum of 34. The month with the minimum salinity recording is again a spring month, namely March 1951, when an observation of 11 ‰ was recorded.

One interesting feature of the year-by-year monthly comparison of salinity variations is the rather marked variation in the range of salinity for a given month from year to year. For example, in January 1952, the salinity varied between 16 and 34 ‰ as compared with the change between 29 and 37 ‰ the following year. The reason for these variations can be correlated again with discharge values for the Mississippi River. Thus, any remedial measures involved in corrosion and fouling control of offshore platforms in floating equipment, can be predicted and planned for in terms of changes in the stages of the river.

The monthly variation in air and sea temperatures are shown in Figure VII. The reason for air temperatures being lower than sea temperatures during the summer months is caused by the fact that these temperatures were observed between 6 and 7 A.M., before the temperature of the air had an opportunity to exceed that of the water, which it did later on in the day. The variation by months from year to year is evident, also, in this figure, although the general pattern of annual variation is nominal for the area. This temperature information should be of interest to meteorologists and oceanographers studying heat-budget relationships of the Gulf of Mexico, as well as to marine biologists.

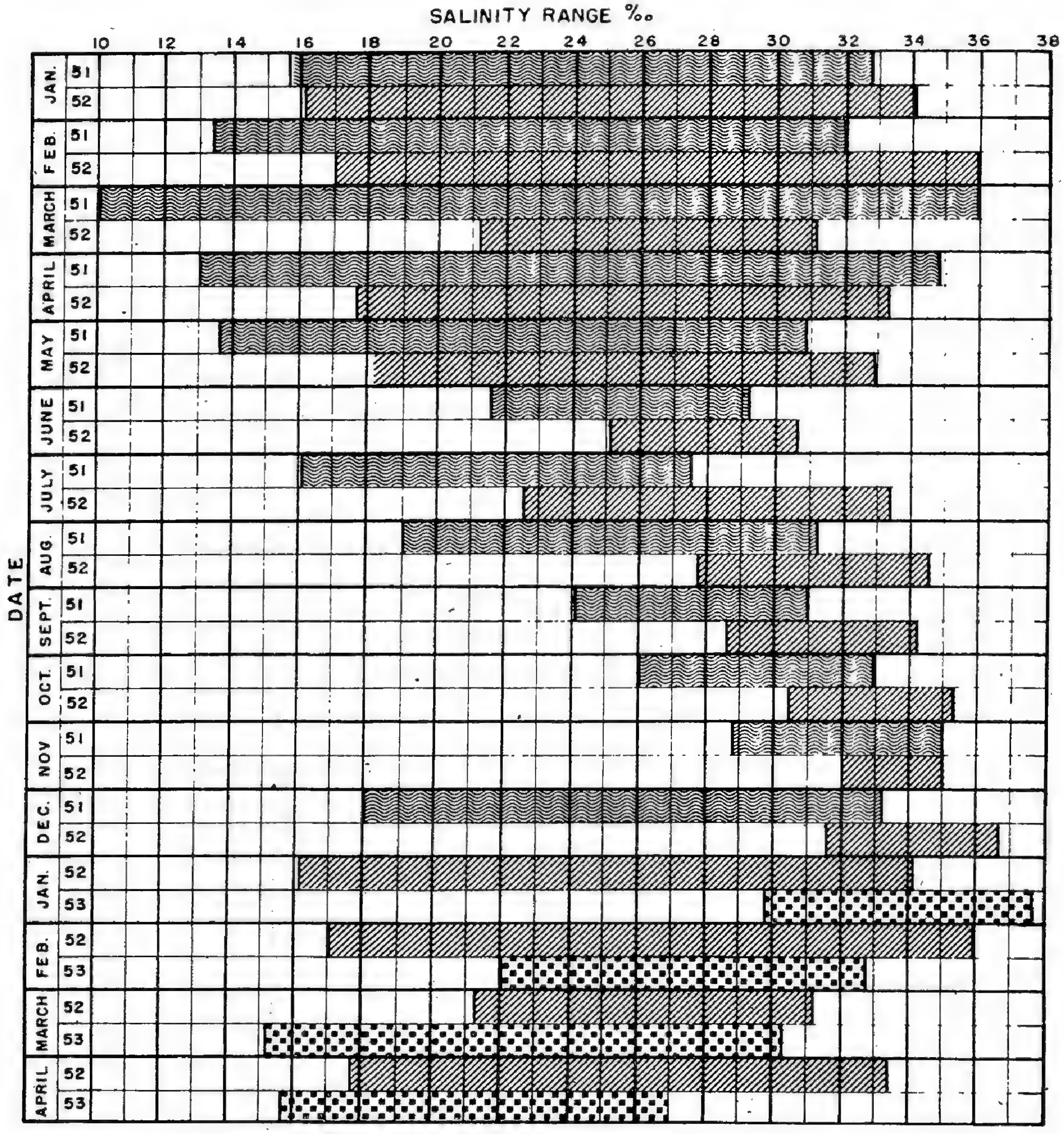
Figure VIII is presented because it shows clearly the reversed thermocline, with colder water at the surface, which holds for the northern Gulf in the winter.

2. CORROSION

There was an intimate connection between fouling and corrosion and the pattern seemed to be clear and simple. The fouling mat covering the surfaces of the two top cylinders, did not always cover the third cylinder completely and left from half to three-fourths of the bottom cylinder bare. Rust appeared only on the bare places and thus was inversely proportional to the amount of fouling. The merest film of rust appeared and as a corrosive process rusting appeared to be minor, at least at lower levels. The fouling mat was underlaid completely with black powdery material, arising in some places as pustules covered with a crust. The steel underneath was pitted. This strong corrosive process was directly proportional to the amount of fouling. Studies of this process by Caldwell and Lytle (1953) have shown that the black material is, strangely enough, aragonite darkened by iron sulphide and is deposited by sulphate reducing bacteria. These organisms operate under anaerobic conditions to cause heavy corrosion of steel surfaces under the fouling mat and thus heavy corrosion and heavy fouling go together.

The point is of particular significance because it indicates the possibility that if fouling could be prevented, corrosion of bare steel in sea water would be greatly reduced.

Table 2 gives a schematic representation of the relative proportion of fouling, anerobic corrosion, and rust on the cylinders at various levels.



MONTHLY RANGE IN SALINITY ‰ (Parts Per Thousand)
GRAND ISLE "A" PLATFORM - JANUARY 1951 - APRIL 1953

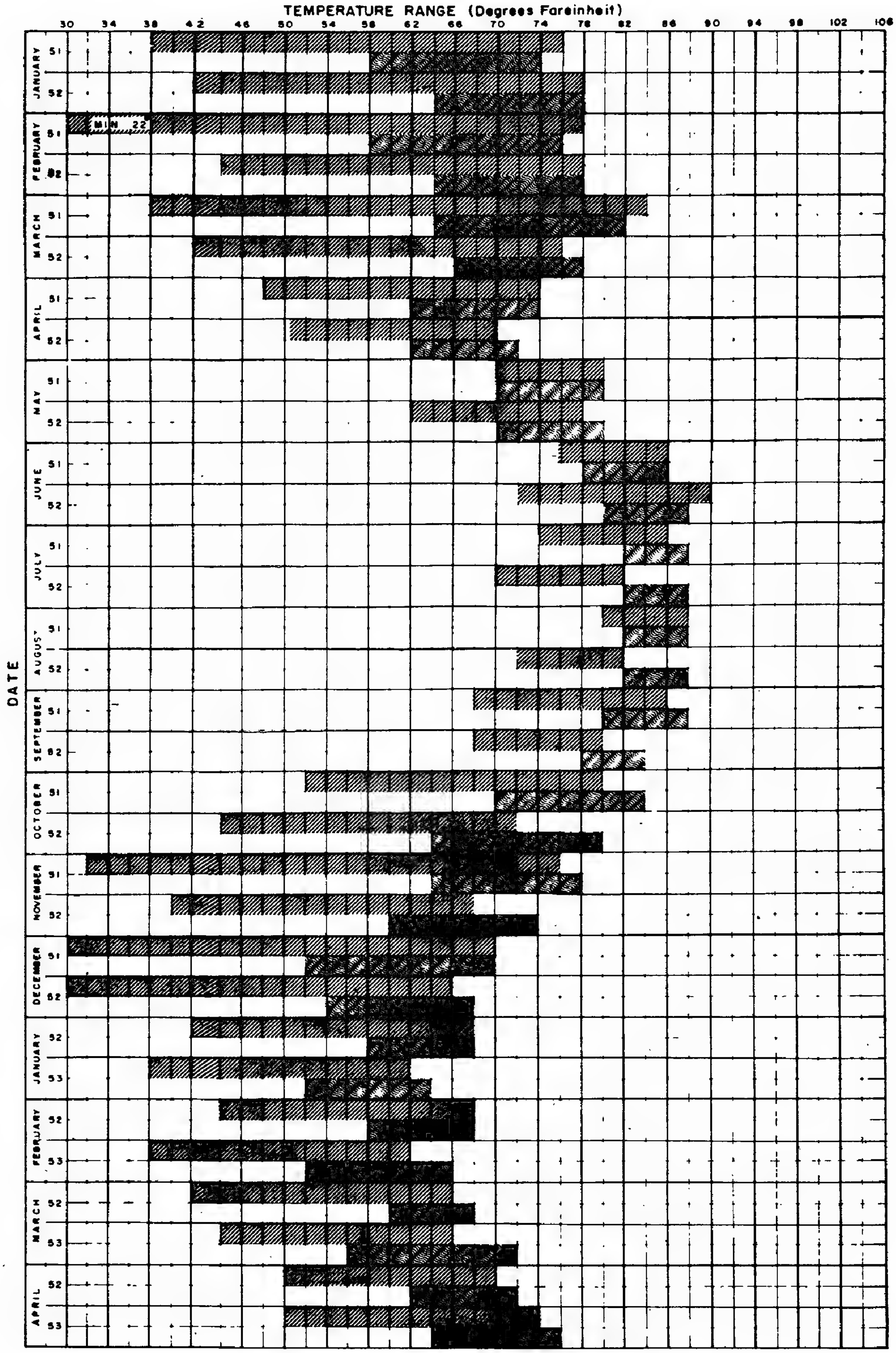
LEGEND

▒ 1951

▨ 1952

⁘ 1953

FIGURE VI



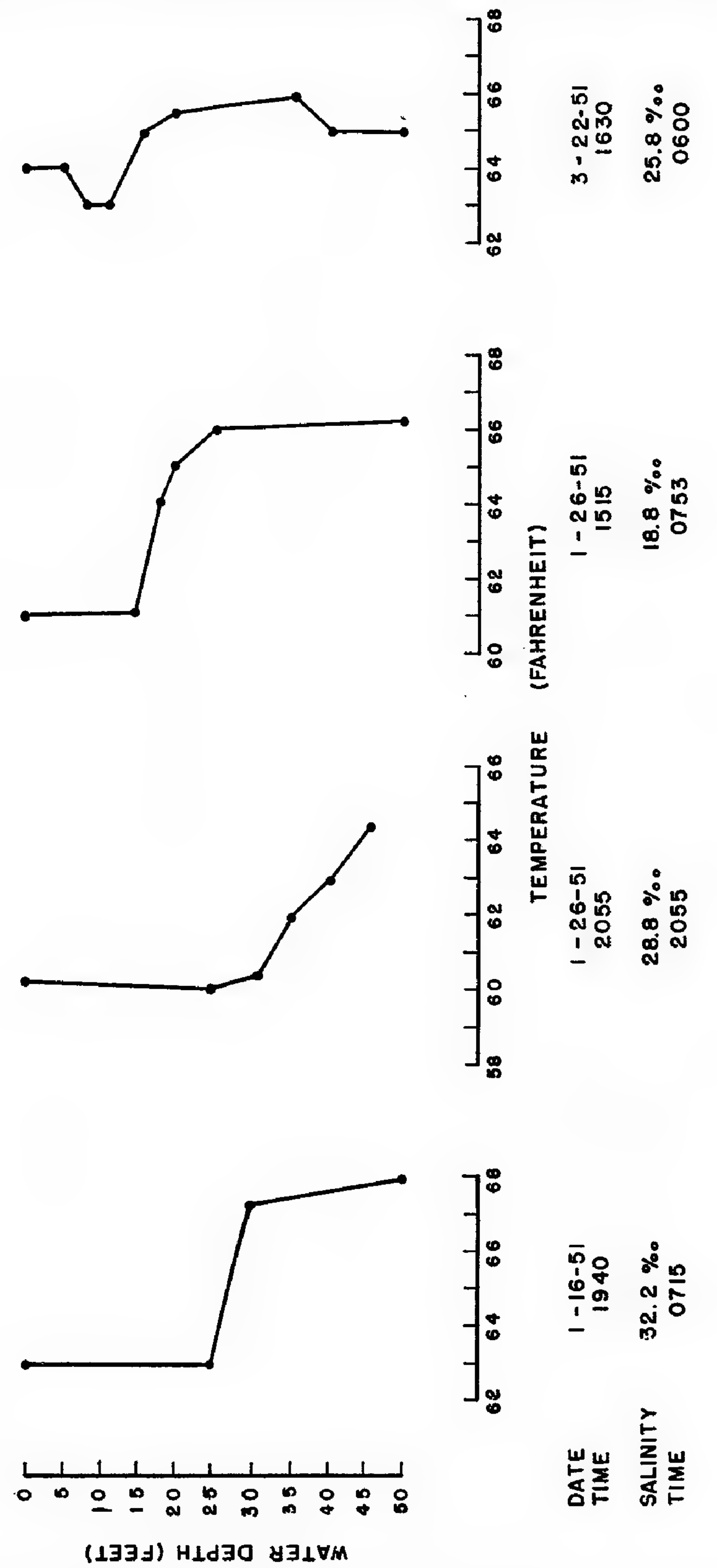
MONTHLY TEMPERATURE RANGE
GRAND ISLE "A" PLATFORM-JANUARY 1951-APRIL 1953
TEMPERATURES OBSERVED BETWEEN 6 AND 7 A.M.

FIGURE VII

LEGEND
▨ AIR TEMPERATURE
▩ SEA WATER TEMPERATURE

3. FOULING ORGANISMS

The fouling organisms can be divided easily into two groups, the less abundant and the more abundant. The former were taken only a few times, while the latter were always present and usually in great numbers. In fact, a fairly adequate description of the fouling can be given with attention only to the more abundant organisms. Nevertheless, the less abundant organisms give certain auxiliary information and are of interest for their own sake. They are treated first.



BATHYTHERMOGRAMS AND SALINITIES
OBSERVED AT HUMBLE GRAND ISLE PLATFORM "A"
29° 10' N.: 89° 54' W.

FIGURE VIII

TABLE 2

A Schematic Representation of Proportion of Fouling, Anaerobic Corrosion and Rust on the Cylinders.

Cylinder	Fouling	Corrosion	Rust
Top	+++	+++	0
Second	+++	+++	0
Third	++	++	+
Bottom	+	+	++

a. *Less Abundant Organisms*

The bryozoan, *Acanthodesia,* was the most common or most often seen of the less abundant organisms. It occurred variously as a very thin encrustation in single patches about one inch in diameter or covering over three-fourths of a cylinder. Its distribution between the two platforms varied considerably and at times there were none on the changed collectors at one platform or the other. This can be seen in Table 3. A peculiar fact was that these little animals were found at times at all depths. Nevertheless, the greatest abundance was always on the bottom cylinder, and this too varied from one platform to the other. This raised the suspicion that depth, light and salinity were not limiting factors to setting and growth, since the organism showed ability to grow at all depths, but that competition with other larger faster growing fouling organisms limited it instead, and thus it grew best near bottom where other animals were comparatively scarce.

TABLE 3

The Distribution of the Bryozoan, *Acanthodesia,* on the Collectors at Both Platforms.

	March 27, 1951		*July 18, 1951*		*January 29, 1952*		*14 mo. samplers*	
	G.I.A.	*Caminada*	*G.I.A.*	*Caminada*	*G.I.A.*	*Caminada*	*G.I.A.*	*Caminada*
1	few	few	0	0	0	0	few	0
2	few	few	0	0	0	0	0	0
3	few	few	0	0	several	0	0	0
4	abund.	abund.	0	abund.	abund.	0	0	several dead
Plate	....	....	few	few	few	few	....	....

TABLE 4

Numbers of Serpulid *(Eupomatus)* Worm Tubes on Bottom Cylinders at All Stations

March 27, 1951		*July 18, 1951*		*January 29, 1952*		*14 mo. samplers*	
G.I.A.	*Caminada*	*G.I.A.*	*Caminada*	*G.I.A.*	*Caminada*	*G.I.A.*	*Caminada*
few	few	19	128	few	0	few	55

Serpulid worm tubes of the genus, *Eupomatus,* were found on the bottom cylinders only and were found on all of them except one at Caminada. The numbers are shown in Table 4. Some factor, such as low salinity of surface waters, limits the distribution of these worms sharply. The greatest abundance was found in July, 1951, indicating a spring spawning peak.

The little shallow water coral, *Astrangia astreiformis,* was found only on the 14 months samplers at Caminada. One patch was found on the second cylinder, 24 on the third and a few scattered ones on the bottom. Thus the best depth for the coral seemed to be about thirty feet. This coral prefers salinities near that of pure sea water and complete absence at Grand Isle A may have resulted from the fact that that area was less saline than Caminada. Absence from the six months collectors is some indication that no setting took place at Caminada between July 18 and January 29.

A beard of green filamentous alga was found growing on the upper cylinder and flat plate at Caminada on July 18. A very small wisp of this plant was found on the upper cylinder of the changed series on January 29. This was the only plant fouling material observed during the investigation. The Caminada platform is not as large as Grande Isle A and permits more light to strike the collectors, which possibly explains the absence of the alga from Grand Isle A.

Several mollusks constituted the remainder of the rare or uncommon organisms in the fouling complex. These were of several species. Four small *Crepidula* were found on cylinders 3 and 4 at Grand Isle A and on 4 (the bottom) Caminada, on July 18. One wingshell, *Pteria colymbus,* was found on the third cylinder of Grand Isle A on July 18. One arc shell, *Arca campechiensis,* was found on the bottom at Grand Isle A on the same date. Eleven *Arca transversa* were found on the same cylinder and one was found on the third Caminada cylinder on the same date. Three specimens of two species of oysters were found. A flat oyster, *Ostrea equestris,* was found on the bottom at Grand Isle A on March 27. Two more were found on cylinders 3 and 4 of that platform on July 18. The largest oysters on the two dates were 35 and 32 mm. long and had grown at rates of 0.28 mm. per day from November to March and 0.29 mm. from March to July. The average daily growth of a man who grows to 6 feet in 18 years is 0.28 mm. per day. One common oyster, *Crassostrea virginica,* was found on the surface cylinder at Caminada on January 29. It was 35 mm. long. The presence of *Crassostrea* at the surface and *Ostrea* lower down is to be expected from the general salinity tolerance of the two species, *Crassostrea* being more estuarine.

Two motile or crawling organisms were sometimes found on the samplers. These were the oyster borer, *Thais haemostoma,* and the stone crab, *Menippe mercenaria.* Neither of these animals can swim and those found on the flat plates certainly settled as larvae. Three *Thais* were found on the flat plate and eight on the second cylinder at Grand Isle on July 18. One was found on the plate and two on the third cylinder at Caminada on the same date. The lengths of these little snails ranged from 3 to 12 mm. A specimen 14 mm. long was taken from the surface of the 14 month collectors on January 29 at Caminada. Small stone crabs were taken from both flat plates on July 18. There was one at Grand Isle A and 30 at Caminada. One was taken at the surface at Caminada on January 29. The carapace widths of these little crabs ranged from 5 to 8 mm.

In summary: Of the less abundant organisms, *Crassostrea,* a green alga, and the creepers, *Thais* and *Menippe,* preferred upper levels. The mollusks, *Ostrea,* two species of *Arca,* and *Crepidula,* the serpulid worms, *(Eupomatus)* the coral *(Astrangia)* and the bryozoan *(Acanthodesia)* preferred or grew most abundantly at lower levels. In this group only *Acanthodesia* was taken at the surface.

b. *Abundant Organisms*

The abundant organisms were *Corophium,* hydroids, barnacles and anemones. They dominated the fouling fauna in numbers and mass.

Corophium lives in little tubes of its own mud deposit or crawls around in the forest of hydroids. The animal feeds on plankton which it strains from the water. In this connection it deposits the suspended sediment and debris in large amounts. These organisms are quite small and are often hidden, so that quantitative amounts are difficult to make. They are not sessile or attached and can swim, although they usually crawl about on the substratum. Table 5 gives the comparative abundance on the various samplers. It was estimated that the ranks numerous to abundant ranged from 1200 to 7500 animals per square foot. However, it must be admitted that these estimates may be off by a large percentage. A breakdown of this table shows that at the upper cylinders the animal was recorded as abundant seven times, numerous twice, present five, few once and absent once. On the two bottom cylinders it was recorded as abundant twice, numerous twice, present four times, few four times and absent three times. Clearly *Corophium* was most abundant at the upper levels.

There was some slight indication that *Corophium* moved to lower levels in winter. It was recorded as abundant twice at the two lower levels on January 29 but was not listed as abundant at these levels on March 27 and July 18.

Under some conditions hydroids grow several inches or up to a foot high. On the cylinders and plates used in this work they were exposed to grazing by fish and to wave action and they grew only as a short fuzz an inch high or less, of varying density. In a few instances colonies inside the cylinders grew into short tree-like forms a few inches high. There are a few hundred species in the marine waters of North America and those in the Gulf are not well known. The identification of species is difficult. Mr. M. D. Burkenroad identified some of the genera involved as *Halecium*, *Bougainvillea* and *Campanularia*. Others were probably present, but they have not been identified. For the purposes of this investigation the identification "hydroids" was deemed sufficient.

TABLE 5

Comparative Abundance of *Corophium* on Various Fouling Collectors. In the Lower Section They Are Arbitrarily Ranked by Abundance with One Being Most Abundant.

	March 27		*July 18*		*January 29*		*14 Mo. samplers*	
	G.I.A.	*Caminada*	*G.I.A.*	*Caminada*	*G.I.A.*	*Caminada*	*G.I.A.*	*Caminada*
1	present	present	abund.	abund.	num.	abund.	present	abund.
2	abund.	abund.	not seen	num.	abund.	present	present	few
3	present	present	few	none	abund.	present	few	few
4	none	present	not seen	none	num.	few	abund.	num.
Plate	Abundant		Numerous		Present	Few	None	
1	4		1		3	0	0	
2	3		1		2	1	1	
3	1		0		3	3	1	
4	1		2		1	1	2	

Table 6 shows that the hydroids decrease from the top to bottom. There is some indication that in summer the abundance declines. Winter is the period of greatest abundance. Coe and Allen (1937) found that hydroids at the Scripps Institution pier declined in abundance in summer and reached a peak in late fall and early winter.

Barnacles on the collectors all belonged to the species *Balanus improvisus*, except two specimens of *B. amphitrite* found on the square plate at Caminada on July 18. There are four more or less common barnacles on the Gulf Coast. *B. improvisus* seems to be the most estuarine and it is sometimes found quite far inland in the brackish water lakes. Why other species of barnacles were not taken on the deeper cylinders, where the salinities were highest, is not known. Not a great deal is known about factors influenc-

Table 6

Relative Abundance of Hydroids on All Cylinders, Listed in Arbitrary Rank of 1, 2, etc. With One Being Most Abundant.

	March 27		*July 18*		*January 29*		*14 Mo. samplers*	
	G.I.A.	*Caminada*	*G.I.A.*	*Caminada*	*G.I.A.*	*Caminada*	*G.I.A.*	*Caminada*
1	1	2	2	1	1	1	1	1
2	2	1	3	2	2	2	2	2
3	3	3	3	2	3	3	3	3
4	4	4	4	2	4	4	4	4
Plate	....	....	2	2	1	1	1	1

ing the life of barnacles after they set. They are known to set however in large numbers on various substrata, live for a short time and then die. That pattern was often followed on the cylinders and no barnacles grew to large size. In many cases the majority were dead when examined.

Table 7

Estimates of Numbers of Barnacles *(B. improvisus)* Per Square Foot on the Cylinders and Plates. These Were Made by Counting the Numbers Present in Units of 4 to 6 Inches and Multiplying by the Area.

	March 27		July 18		January 29		14 mo. samplers	
	G.I.A.	Caminada	G.I.A.	Caminada	G.I.A.	Caminada	G.I.A.	Caminada
1	9500	7800	3400	90	110	2595	295	few
2	6100	6100	3400	4200	340	2880	60	900
3	9600	8000	2000	6650	245	1440	785	5180
4	85	3900	65	0	0	1150	575	0
Plate	....	1200	1950	180	26	....	....	....

Table 7 shows the numbers of barnacles taken on the collectors. The numbers taken on cylinders 1, 2, 3 and 4 (all samples) were approximately 25,000, 24,000, 34,000 and 6,000. Few barnacles were taken on the bottom cylinder except at Caminada. The mass of barnacle fouling was greatest at the upper two cylinders. Most of the vast numbers found on the third cylinder were only 2 mm. across, while on the upper cylinders the sizes were 10 to 14 mm.; in addition most barnacles on lower cylinders were dead. It appears that barnacles set in numbers on the third cylinder, lived a short while and died. On March 27 very few dead barnacles were seen. On July 18, almost exactly 90 per cent were dead. On January 29 about 88 per cent of the barnacles were dead. The reasons for this mortality are unknown, but it is possible that competition with anemones had something to do with it.

Table 8 shows the counts of anemones on the collectors. On March 27 anemones

Table 8

The Counts of Anemones on all Fouling Collectors are Shown. Inside and Outside are Combined.

	March 27		July 18		January 29		14 mo. samplers	
	G.I.A.	Caminada	G.I.A.	Caminada	G.I.A.	Caminada	G.I.A.	Caminada
1	few	few	100	none	1700	plastered	8600	plastered
2	few	few	3900	5200	9200	5500	plastered	plastered
3	few	few	6100	5400	4850	5900	7700	7200
4	none	none	none	none	4850	plastered	6500	6400
Plate	....	....	1540	6600	4900	5–10,000	....	....

were small and few and were characterized as smaller components of the fouling complex. They increased from then on and at the last were the most massive part of the fouling. The heaviest layer was on the inside of the cylinders, where at some depths they completely plastered the surface, leaving no room for hydroids and covering the barnacles. In many instances they grew within the cones of dead barnacles. Anemones at the lower levels were mostly small pink ones *(Anthopleura krebsi)*. Those at upper levels were largely brown anemones *(Aiptasia pallida)*. Anemones on the plates and on the outside of the cylinders were smaller than those on the inner surface. Probably this was due to better protection from grazing fish on the inside of the cylinders. The greatest amount of anemone material was on the upper levels, a fact not discernible from the counts, because at those levels individuals were larger.

Anemones obliterated and grew over all other fouling organisms on the inside of the cylinders. They certainly obliterate hydroids and *Corophium* and also cover the barnacles. Whether they grow over the barnacles after these are dead or smother them out is unknown, but it seems probable that they kill the barnacles by overgrowth. The live barnacle population decreased as the anemone mass increased. This can be seen by a comparison of tables 7 and 8.

The total mass of fouling on the collectors put down on July 18, which were down 6½ months, was greater than that on the unchanged samplers which were down 14 months. The reasons are unknown. The substrate may have become covered with a thin gel of bacteria or diatoms before larvae of the fouling organism appeared in the water. This would have prevented setting of larvae and resulted in diminished fouling, at least for a period of time.

Figure IXa is a photograph of all Grande Isle A cylinders from top to bottom. The cylinder with white patches *(Acanthodesia)* is the bottom one. Figures IXb, c, and d. show the inside of the top, second and bottom cylinders, respectively. These cylinders were put down on November 27, 1950 and raised March 27, 1951. They were photographed on April 4, 1951.

c. *Second Year's Observations*

A second set of cylindrical collectors were put down on April 22, 1952 at both platforms and another flat plate was placed at Caminada. The plan was to leave the collectors down for one year, so as to compare the fouling with that of the previous long term samples. The collectors were raised and examined on May 11, 1953. The results are briefly stated here:

Grand Isle A.

Top collector.—This cylinder was covered with a mat of hydroid fuzz one-fourth to one-third of an inch long. It covered the barnacles and made them hard to count, but they were few in number. The small amphipod, *Corophium*, was enormously abundant.

Second cylinder down.—So far as hydroids went, the outside of the cylinder was much the same, but they were much less thick on the inside, apparently because of competition with anemones which were much thicker. *Corophium* were also considerably less abundant. Barnacles were few.

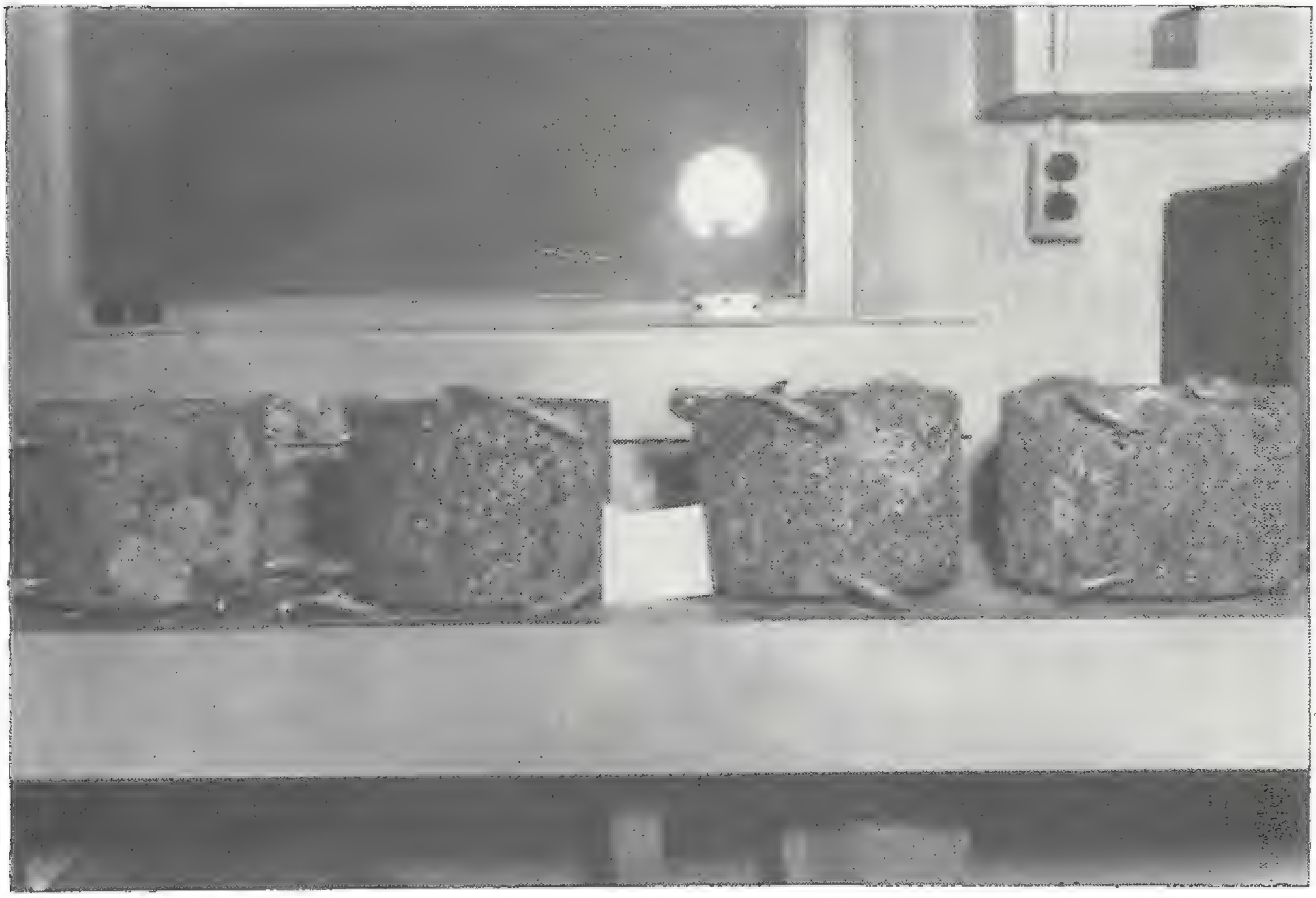


FIG. IXa. A photograph of all cylinders from platform Grand Isle A from top to bottom, the cylinder with light patches being the bottom.

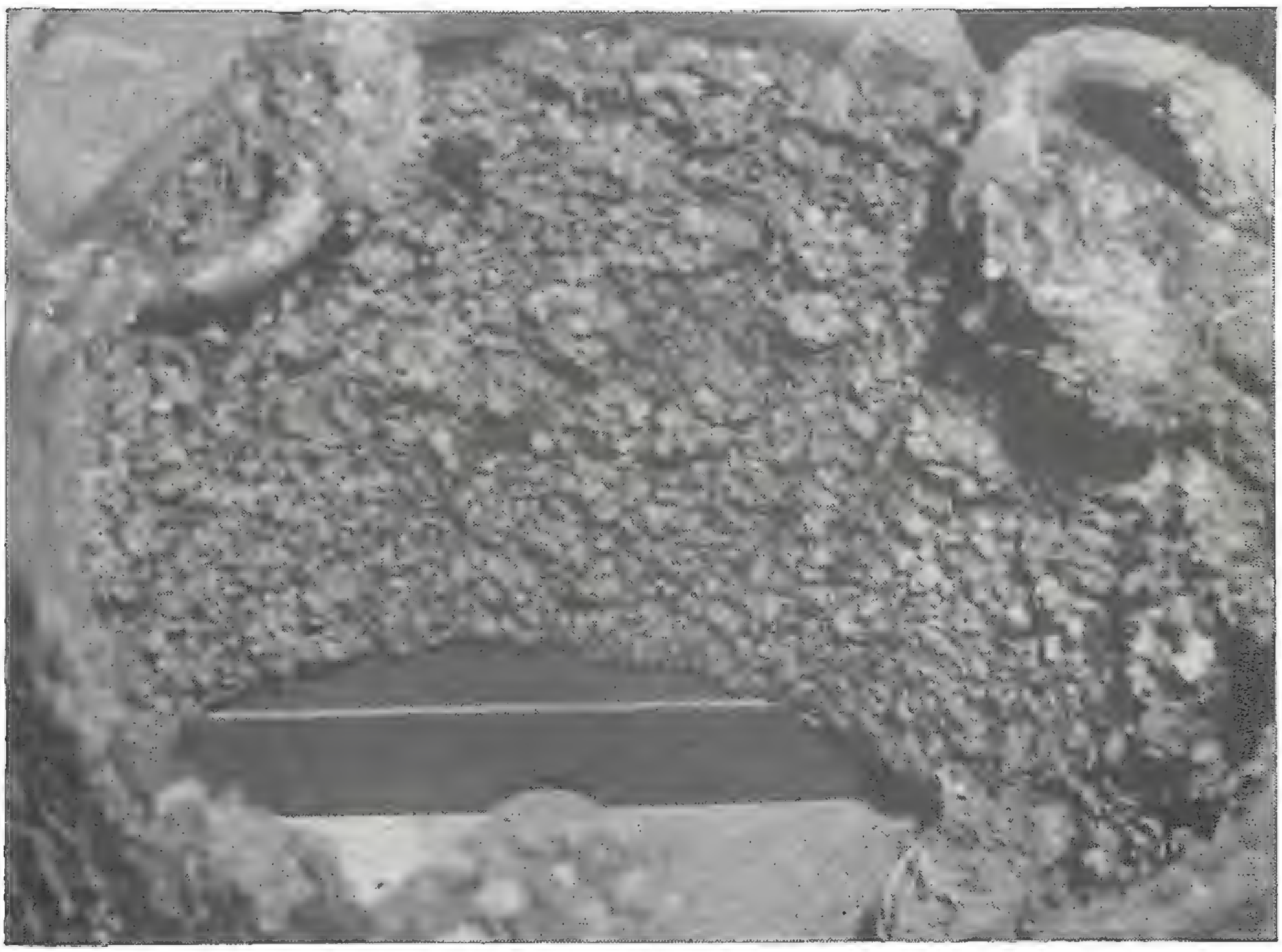


FIG. IXb. A photograph of the inside of the top cylinder. Both photographs were taken eight days after removal from the water. The collectors were down from November 27 to March 27.

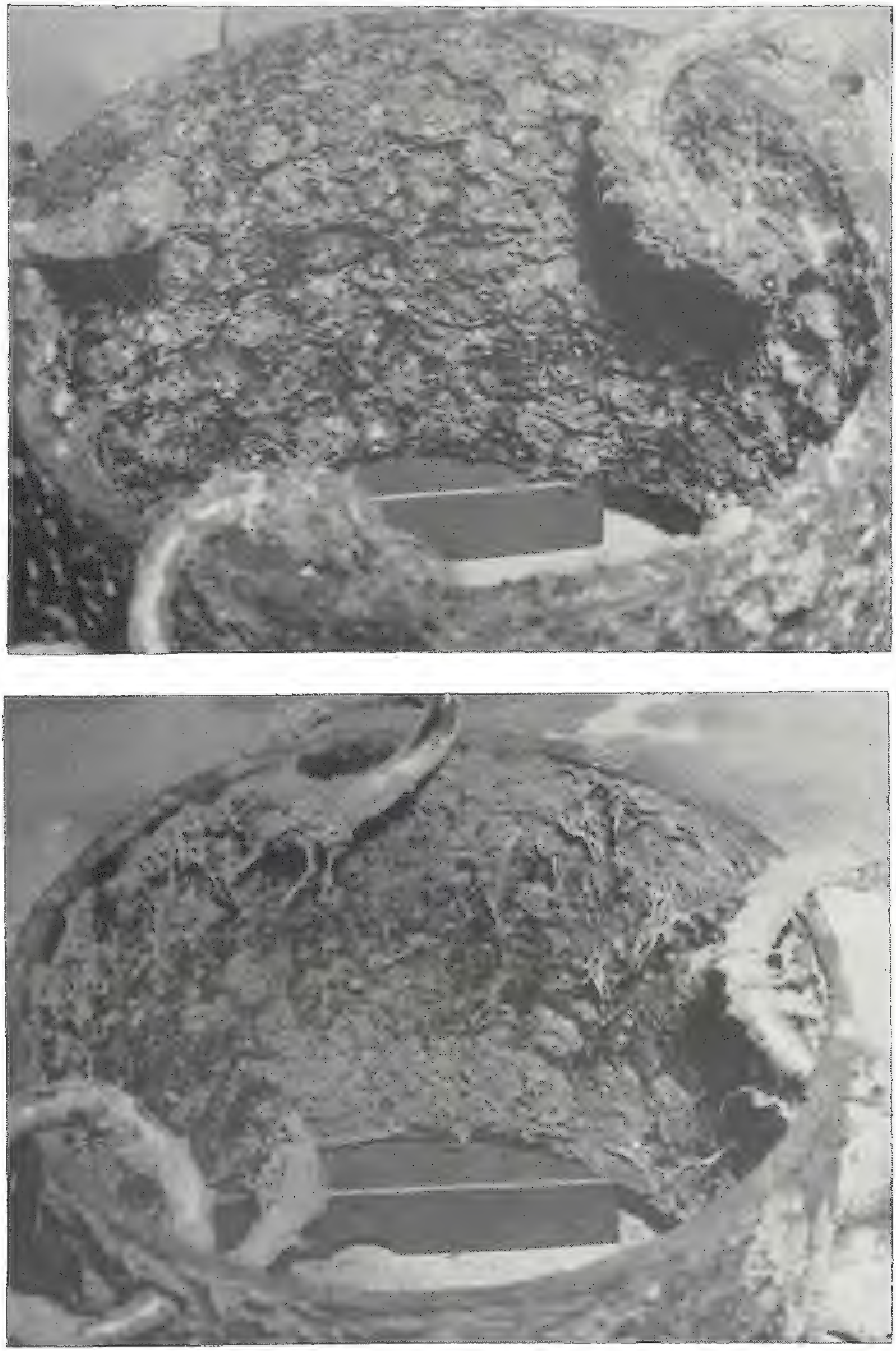


Fig. IXc (top) and IXd (bottom). Photographs of the inside second and bottom cylinders, same set as IXb.

Third cylinder down.—Hydroids and anemones were much less abundant. *Corophium* was present and in general fouling was less, except for the barnacles, which were about the same. One calcareous worm tube was present on the inside. It belonged to *Eupomatus dianthus.*

Bottom cylinder.—The wire rope had worn in two and the collector was missing. Caminada A.

Top cylinder.—This cylinder was covered with a short hydroid fuzz on the outside and anemones were practically absent. There were less hydroids and more anemones on the inside. *Corophium* was abundant on both surfaces, but thickest on the inside. Few barnacles were present.

Second cylinder down.—Barnacles were thicker than on the top cylinder on both surfaces, especially on the inner, where they were a solid mat in some places. Hydroids were thin exteriorly and practically absent inside. *Corophium* were abundant outside and enormously abundant inside.

Third cylinder down.—Barnacles and hydroids were less common than on the above cylinder. *Corophium* was present in vast masses; in places they had deposited a complete covering of sediment with little holes to the surface.

Bottom cylinder.—The outside cylinder was clean except for rust spots and a little patch of hydroids near the top. However, this surface looked as if it might have rubbed against something else. The inside was covered with strands of the bryozoan, *Bowerbankia,* up to three inches long. Where this bryozoan was shorter about 60 calcareous worm tubes stood upright and protruding through the mat. Two *Crepidula glauca,* one small prosobranch gastropod and two small peleycypods, *Arca transversa,* were found in the mat. There was a patch of encrusting bryozoa, *Acanthodesia,* covering about four square inches. Barnacles, anemones and hydroids were absent.

The flat plate.—A flat steel plate one foot square was suspended at a depth of about ten feet off Caminada A. Examination showed a relatively thin hydroid fuzz, 150 barnacles per square foot and about 2800 anemones per square foot. *Corophium* was present but not in great abundance. One barnacle, *Balanus eburneus,* was 35 mm. across.

General Results.—The fouling mat was complete on all collectors except the bottom one at Caminada. In general the hydroids were less thick where anemones were thinner and vice versa. At Grand Isle A anemones were most abundant on the upper two cylinders, but at Caminada they were found in greatest numbers on the second and third. Similarly, barnacles were more abundant at Caminada on the second and third cylinders. Anemones were smaller and more numerous generally on the outer surface of the cylinders, except for the surface cylinder at Caminada which was covered with a thick hydroid fuzz. They were larger and less numerous on the inner surface. Probably this smaller size on the outside is due to grazing by fishes on the outer surfaces. Similar differences among the barnacles were not noted.

Barnacle mortality was about 20 per cent. Barnacles varied in size from about 10 to 35 mm. in basal diameter. No small barnacles were found and apparently there had not been a set that spring. All barnacles examined contained developing eggs in early stages. The barnacles were all *Balanus improvisus,* except for two *B. eburneus.* The anemones were *Aiptasia pallida.*

Comparisons with the Previous Year.—In general these collectors showed the same fouling pattern as the previous year. The dominant organisms were the same and the fouling mat was solid on all cylinders except the bottom one. Worm tubes, bryozoans and other less numerous organisms were similarly found only on the lowest cylinder. Their variety was somewhat less. No filamentous green alga was found at Caminada, as on the temporary collectors at this location. The oyster borer, *Thais,* and the stone crabs, *Menippe,* were absent from all cylinders. Anemones were smaller in size and in general not so prolific as in the previous year. No pink anemones, *Anthopleura krebsi,* such as were reported during the previous year, were found.

TABLE 9

Numbers of Barnacles and Anemones Found on the Fouling Collectors Down From April 22, 1952 to May 11, 1953.

	Grande Isle A		Caminada A	
	Outside	Inside	Outside	Inside
Top				
Barnacles	60 large	120	20	125
Anemones	1944	1296	very few	2924
Second Down				
Barnacles	60	100	286	800
Anemones	3744	1872	4464	542
Third Down				
Barnacles	75	130	144	288
Anemones	1584	864	2880	3456
Bottom				
Barnacles	Cylinder Missing		none	none
Anemones	Cylinder Missing		none	none

Comparison of Table 9 with Tables 7 and 8, the previous year's sample, shows that barnacles were not present in great numbers and were more evenly distributed from top to bottom and from inside to outside on these later collectors. It also shows that anemones were much more abundant on the first year's collectors. In general the fouling growth on the last set was not so luxuriant. Possibly this is because the first collectors were actually in the water fourteen months and were raised in January. Fouling growth seems to be heaviest in midwinter.

GENERAL CONSIDERATIONS

A. Fouling Organisms and Salinity

During the period covered by this work the temperature of sea water and the salinity at a depth of approximately ten feet was determined daily at Grand Isle A. The temperature followed the usual cycle with the low in January ranging from 59 to 67° F. with a high in August ranging from 83 to 88° F. The salinity ranged from 10.0 to 37.0 parts per thousand, with the lowest salinity coming in the early winter and spring and the highest in the late summer and fall. The data collected during this time are much less complete than those presented by Geyer (1950). He has shown that marked seasonal and short term variations in salinity take place at Grand Isle A and other similar platforms in the Gulf.

It is clear that the fouling animals growing in the upper water levels live in what might be termed a highly saline estuarine condition. This environment has been called polyhaline. The anemones, the barnacle, *Balanus improvisus*, the common oyster *Crassostrea,* and the oyster borer, *Thais,* show the polyhaline nature of the upper water levels.

Unfortunately, there are no salinity records for the water layers near bottom. However, the presence of tube worms, *Eupomatus,* the arc shells, the oyster, *Ostrea,* and the coral, *Astrangia,* at the lower levels indicate that the salinity averaged higher near the bottom than at the surface. This means, of course, that it was less variable and more similar to pure sea water than the surface layers. The tube worm, the coral and *Ostrea* grew at upper levels of platforms off the Texas coast. They have also been reported from the very shallow waters of high salinity bays (Gunter, 1950). Thus, it seems they are not confined to deeper water off the Louisiana coast because of depth, light or any other factor except salinity.

On the Louisiana platforms the surface to bottom distributions of organisms is in part a telescopic replica of the horizontal distribution from the mid-bays to the open sea, covering several miles, as has been shown by Gunter (1950), Ladd (1951) and Hedgpeth (1953). The same thing is shown to some extent on the Texas platforms. Presumably, this top to bottom duplication of horizontal distribution from estuarine (polyhaline) waters to sea water will fail to hold on platforms in areas of higher salinity. Some indication of this is given by the growth of high salinity organisms at upper levels on the Texas platforms.

Animals which live in an environment of variable salinity have their reproductive cycle of spawning in tune with the temperature cycle rather than salinity (Cf Gunter, 1945, 1950). Therefore, as was expected, no particular correlation between setting of the fouling organisms in the months of high or low salinity were discovered in this work.

B. Succession

Tables 5, 7 and 8 and general observations show that barnacles, hydroids and *Corrophium* set on the collectors fairly early and there was no evidence that they competed strongly with each other, for they were often seen growing vigorously together. In fact, barnacles were usually covered with a hydroid fuzz. As time went on, however, anemones slowly began to increase in size and number and at the end of a year they virtually plastered many collectors, especially on the inside, so that some of the collectors when raised appeared to be covered with a rugose, glistening jelly. After a few hours in the air this jelly became more like a dried membrane and the underlying barnacle remains became more apparent. During the second year of this study, the increase of anemones did not proceed so far, but the tendency was apparent. Thus, it may be said that as time goes on anemones definitely supersede the barnacles as the dominant animals in this fouling complex. Whether they form the climax community or are only a seral stage of the microcosm is unknown. Furthermore, it is not known that anemones are direct competitors or are injurious to barnacles, for the multitudinous barnacles are given to dying like proverbial flies at all times and patches of dead barnacles are common sights wherever there is a hard substrate along the seashore. The general causes and reasons for the mortalities of the vast hordes of barnacles is one of the unwritten chapters of marine biology, and except for the fact that we can surmise that the clouds of larvae must often set where the environment is not continuously suitable, little is known. Possibly, the anemones flourish only after the barnacles have died from other causes.

SUMMARY

A study of fouling organisms was made off the Louisiana and Texas coasts.

Observations on templates of pulled oil-well platforms, from offshore waters of Louisiana and Texas, in depths of 6 to 10 fathoms were made between July 1949 and February 1950. Barnacles, a fuzz of hydroids, the horse oyster, *Ostrea equestris* and the bryozoan, *Acanthodesia,* dominated the complex on the lower twenty-five feet of the Texas platforms. Common oysters, *Crassostrea virginica,* were present at upper levels. A green alga was present near the waterline. *Crepidula, Arca* and pinnids were incidental at lower levels. The Louisiana platforms were similar, except that one had no oysters, and the other had *C. virginica* at upper levels with *O. equestris* and *O. frons,* the tree oyster, at lower levels. The coral, *Astrangia,* was taken at lower levels. The saliniphilous organisms were taken at lower levels and the more estuarine organisms, such as the Virginia oyster, were taken nearer the surface. These were growing at five miles offshore and beyond, indicating that upper layers of water were estuarine in nature. The oyster shells contained none of the perforating associates commonly found in the bays. The fastest growth of the oysters was 0.3 mm. a day. In general the top to bottom distribution of sessile animals was a sort of telescoped summary of the horizontal distribution, from estuarine waters to sea water, over a distance of many miles. The same situation was demonstrated on artificial collectors placed on two offshore platforms in Louisiana.

The hull of a ST–7 anchored off the Louisiana coast at distances of five and fifteen miles for fourteen months was examined. A green alga and goose barnacles, *Lepas,* were present at the water line. Common oysters were present on the hull at a concentration equal to about 100 barrels to the acre. Large barnacles, *Balanus tinntinnabulum,* and the wingshell, *Avicula,* were scattered but conspicuous. Thousands of small barnacles, *B. improvisus,* mostly dead, a thick fuzz of hydroids and millions of small anemones were present. A sea-chest in ballast tanks of this boat contained an isolated community of oysters, *C. virginica,* oyster borer, *Thais,* stone crabs, *Menippe* and fish, all much too large to get back to the outside through the half-inch holes through the hull.

Cylinders of eight inch steel pipe, cut so that the outside surface area was one square foot, were strung on steel cables about fifteen feet apart and suspended from two platforms from Louisiana. The depth was about fifty feet, so that the upper cylinder was just beneath the surface and the lower one was just above the bottom. One set at each platform was changed every four to six months for fourteen months, from November 1950 to February, 1952, and a second set was left down for the full period. One flat plate of steel one square foot in area was also suspended from each platform and exchanged every time the cylinders were. A second year's observations were made with a set of cylinders left undisturbed at each platform from April, 1952 to May, 1953.

The fouling mat was complete on the top two cylinders, almost complete on the third and the bottom cylinder was relatively bare. Corrosion and pitting took place under the fouling mat. Presumably, this was caused by sulphate reducing bacteria.

Rusting was greatest at the bottom and was inverse proportion to the coverage of the fouling mat (Table 2).

Certain less abundant organisms, *C. virginica,* the crawlers, *Thais* and *Menippe,* preferred upper levels. A beard of green alga lived near the waterline. The flat oyster, *O. equestris,* two species of *Arca, Crepidula,* serpulid worms, *Eupomatus* and the coral, *Astrangia* were found at lower levels.

The fouling mat was composed of barnacles, *B. improvisus,* hydroids, the amphipod, *Corophium,* and two anemones. These were most abundant on the upper two cylinders. As time went on the anemones slowly became dominant and on some cylinders completely plastered the surface, covering the barnacles and hydroids. Hydroids and anemones grew to greatest size inside the cylinders, probably because they were protected there from grazing fish.

LITERATURE CITED

Caldwell, J. A. and Lytle, M. L. B. 1953. Bacterial corrosion of offshore structures. Corrosion 9(6) : 192–196, 5 fig.

Cary, L. R. 1906. The conditions for oyster culture in the waters of the parishes of Vermillion and Iberia, Louisiana. Bull. Gulf. Biol. Sta., 4: 1–27, 1 chart.

Coe, W. R. and Allen, W. E. 1937. Growth of sedentary marine organisms on experimental blocks and plates for nine successive years. Bull. Scripps Inst. of Oceanog. 4(4) : 101–136, 2 pls., 6 figs.

Geyer, R. A. 1950. The occurence of pronounced salinity variations in Louisiana coastal waters. Jour. Mar. Res., 9(2) : 100–110, 6 figs.

Gunter, G. 1945. Studies on marine fishes of Texas. Publ. Inst. Mar. Sci. Univ. Texas, 1(1) : 1–190, 11 figs.

————. 1950. Seasonal population changes and distributions as related to salinity, of certain invertebrates of the Texas coast, including the commercial shrimp. Publ. Inst. Mar. Sci. Univ. Texas, 1 (2) : 7–51, 8 figs.

————. 1951. The West Indian tree oyster on the Louisiana coast, and notes on growth of the three Gulf coast oysters. Science, 113: 516–517.

Hedgpeth, J. W. 1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. Pub. Inst. Mar. Sci. (Univ. Texas) 3(1) : 107–224.

Ladd, H. S. 1951. Brackish-water and marine assemblages of the Texas coast, with special reference to mollusks. Publ. Inst. Mar. Sci., 2(1) : 125–164, 2 figs. fld. table.

Price, W. A. 1954. Oyster reefs of the Gulf of Mexico. *In* Gulf of Mexico, its Origin, Waters and Marine Life. Fish and Wildlife Service, Fishery Bull. 89: 491.

(Redfield, A. C. and E. S. Deevy, Jr.) 1952. The fouling community. Chap. 3, pp. 35–41. *In* Marine Fouling and its Prevention. U. S. Naval Institute, pp. x+ 388 pp. Annapolis.

Some Phases of the Biology of *Ostrea equestris* Say and a Comparison with *Crassostrea virginica* (Gmelin)[1]

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[1] Contribution Number 25, Oceanographic Institute, Florida State University.

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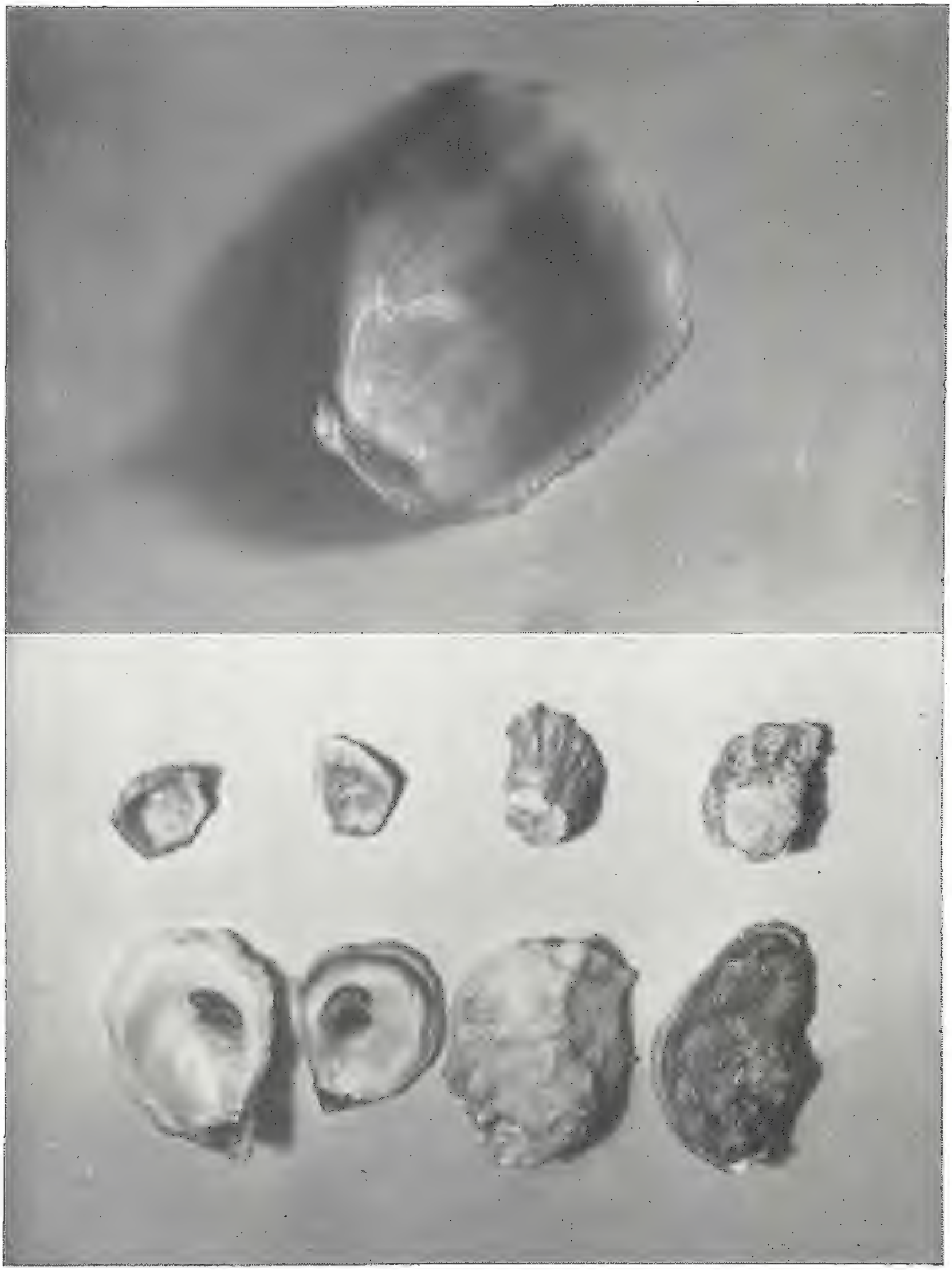


FRONTISPIECE

Shells of *Ostrea equestris* Say and *Crassostrea virginica* (Gmelin), eleven months of age (Growth Experiment I). Upper figure is a photograph of a single left valve of *O. equestris* showing the teeth along the dorsal and ventral edges of shell. Lower figure shows relative size of the two species (upper four *O. equestris*; lower four *C. virginica*) at the age of eleven months.

INTRODUCTION

Oysters, because of their economic importance and their nearly world-wide distribution, have been studied more extensively than any other marine invertebrate. Baughman (1947), Korringa (1952) and Ranson (1952) have compiled bibliographies. Korringa reviewed several hundred papers published since 1940. Publications previous to this date number over five thousand. Despite this voluminous literature, several aspects of the biology of oysters still remain in question.

One of the points in question has been the taxonomic disposition of the two types of oysters of economic importance. Prior to about 1940, all the living oysters were generally considered to belong to two genera: *Pycnodonte* Waldheim, a small genus of no economic importance, and the large *Ostrea* L., which contained all the species of economic importance. Since the publications of Ranson (1939, 1948) and Gunter (1950), it has been generally accepted that *Ostrea* should be divided into two genera. The name *Ostrea* was retained for the larviparous type which has no promyal chamber and which inhabits the more saline areas. The other genus contains the oviparous species which have a promyal chamber, and which are found more abundantly in estuarine areas. This latter genus is called *Gryphaea* Lamarck by Ranson and other European oyster biologists. Gunter (1950) pointed out that the name *Crassostrea* Sacco has taxonomic validity, and it is now used generally. (Dall in 1898 considered this type of oyster to be a subgenus of *Ostrea* and applied the name *Crassostrea* to it.) The name *Crassostrea* will be used here for the oviparous genus.

A tabulation of some of the differences between the two genera is given below. These have all been mentioned in previous investigations.

	Ostrea	*Crassostrea*
1.	Prodissoconch shell with small rounded umbo	Prodissoconch shell with protruding umbo
2.	Average size smaller	Average size larger
3.	Larviparous	Oviparous
4.	Eggs large, number *ca.* 1,000,000	Eggs small, number above 50,000,000
5.	Gill ostia large	Gill ostia small
6.	No promyal chamber	Promyal chamber present
7.	Inhabitants of sea water, high salinity and clear	Inhabitants of estuaries and brackish waters of high turbidity
8.	Muscle centrally located and scar not pigmented	Muscle more posteriorly located and scar pigmented
9.	Left valve flatter	Left valve more cupped
10.	Cleansing mechanisms not well-developed	Well-developed cleansing mechanisms
11.	Shape subcircular; more constant	Shape elongated; more variable
12.	Selectivity of food based on size alone	Discrimination in feeding
13.	Predominantly inhabitants of cold water, but adult unable to withstand freezing *(O. lurida)*	Predominantly inhabitants of warm water, but adult able to withstand freezing *(C. virginica)*

In some places on the Texas Gulf Coast a species of *Ostrea, O. equestris* Say, and a species of *Crassostrea, C. virginica* (Gmelin), occur together (Frontispiece). This affords an opportunity for comparing representative species of each genus under more or less similar natural conditions. It was hoped that such a comparison would clarify some of the discrepancies found in the literature on oysters. It was felt that some of these discrepancies might be due to an attempt to make generalizations for all oysters from observations made on a species from only one of the two genera.

The present study was concerned mainly with an investigation of two phases of oyster biology about which there has been disagreement in the literaure. These are the mode of feeding and the level of attachment in relation to the depth of water. The growth rate, diseases, and predators as well as some of the anatomical details which pertain to the above observations, were also compared. In addition, some observations were made on the life history and embryology of *O. equestris* because this species is little known.

This work was done for the partial fulfillment of the Degree of Doctor of Philosophy in the Department of Biology at The Agricultural and Mechanical College of Texas, College Station, Texas. The writer wishes to thank Dr. Sewell H. Hopkins of this institution, under whose supervision this work was undertaken, for his most valuable help in many phases of the investigations. The summer of 1951 was spent at the Institute of Marine Science, The University of Texas, Port Aransas, Texas, where the writer was employed as Research Scientist. Inspection trips from College Station to Port Aransas were made at approximately monthly intervals from September, 1951 to January, 1953. Thanks are due to Dr. Gordon Gunter, Director, who furnished space and assistance and also to Mr. Martin Burkenroad, of the same institution, for his interest and valuable criticisms. Many others have helped, and thanks are extended to all of them.

METHODS AND MATERIALS

At the Institute of Marine Science, located on Aransas Pass in close proximity to the open Gulf, a wharf extends from the upper end of the jetty and the land of Mustang Island. Investigations were made at a laboratory building on the end of this wharf, over water of a depth of from three to five meters. The culch and growth experiments were suspended beneath the wharf and the other studies were conducted in the building (Figs. 1 and 2).

A series of surface temperature readings and salinity readings were made at the Institute of Marine Science (Table 1). Hydrometer readings were converted to salinity by the use of Knudsen's tables (Knudsen, 1948—reprint).

Two species of oysters occur at Port Aransas, *Ostrea equestris* and *Crassostrea virginica.* A third species, *O. frons.* L., occurs in the northern Gulf east of this region along with the above two species (Gunter, 1951a,b). *O. equestris,* upon which most of the investigations were made, occurs in the Gulf Region and along the Atlantic Coast as far north as North Carolina (the writer studied one sample collected in North Carolina by Mr. M. D. Burkenroad).

PLATE I

FIG. 1. A map of the location of the Institute of Marine Science. The coast line here is almost north and south, perhaps 350° by 170°.

FIG. 2. A view of the platform under the laboratory at the end of the pier of the Institute of Marine Science. The writer is holding the chain to which was attached the culch used in the stratified culch observations.

FIG. 3. Wooden frames used to hold slides to which the oysters attached. The box on the left had been in the water for a period of about one month. Because of fouling and destruction by marine organisms the frames were replaced at intervals by a new frame as shown on the right.

PLATE I

FIG. 1

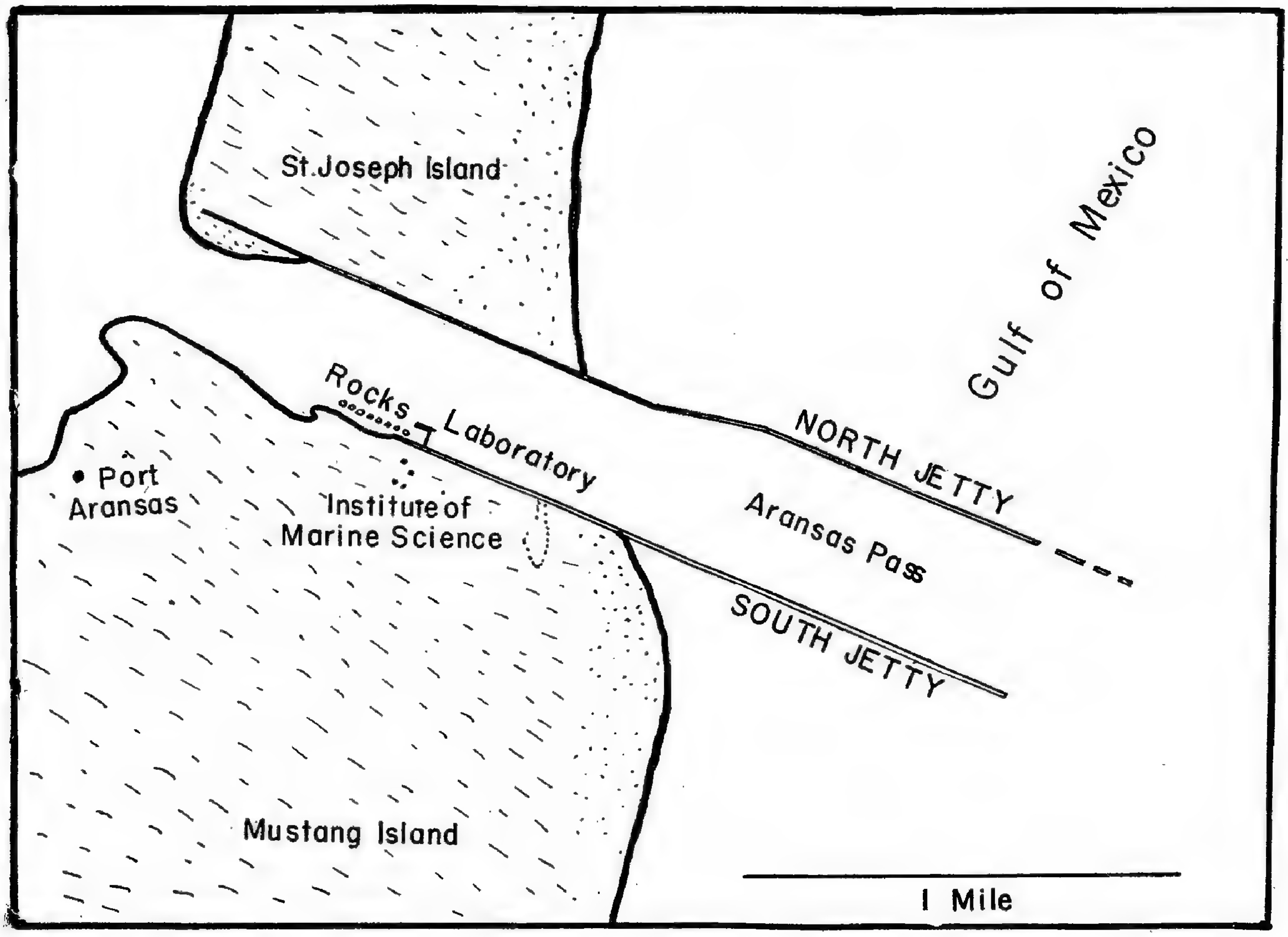
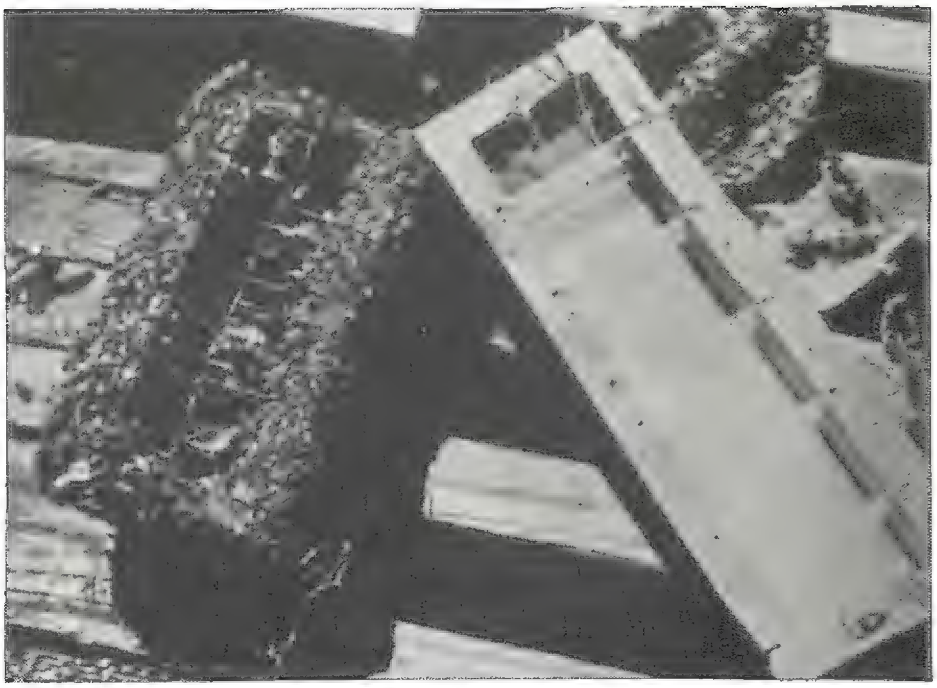

St. Joseph Island
Gulf of Mexico
Rocks
Laboratory
NORTH JETTY
Port Aransas
Institute of Marine Science
Aransas Pass
SOUTH JETTY
Mustang Island
1 Mile

FIG. 2

FIG. 3



Some of the observations were made directly in the field, whereas others involved the use of apparatus both in the field and in the laboratory. Some of the techniques are new; some were modified from previous research. Some of the new techniques can have wider application, and these will be discussed in more detail (especially the observation of small living oysters attached to microscope slides). The methods and materials for each phase of the study will be treated separately, although there is necessarily some overlapping when the same materials were used for several phases.

TABLE 1

Surface Temperature and Salinity Readings at Port Aransas, Texas

Date	Temperature	Salinity	Date	Temperature	Salinity
1951			1951		
August 6	25.5	37.5	September 8	29.9	37.8
August 7	25.4	37.5	September 9	29.6	37.8
August 8	24.9	37.3	September 11	29.4	38.0
August 9	24.5	37.2	September 12	28.6	37.4
August 10	24.8	37.5	September 13	28.1	37.5
August 11	24.4	36.8	September 14	26.8	34.5
August 12	24.4	37.1	September 15	25.5	35.9
August 13	25.7	37.3	September 16	25.2	35.9
August 14	26.9	37.5	October 21	23.9	28.3
August 15	28.1	37.2	December 29	16.1	32.9
August 16	29.2	37.6	December 30	16.0	33.1
August 17	29.6	37.4			
August 18	30.0	37.4	1952		
August 19	29.9	37.6	March 23	19.1	33.5
August 20	29.6	37.1	May 11	21.8	37.2
August 21	30.1	37.7	June 1	26.8	34.9
August 22	29.7	37.3	June 2	26.3	34.5
September 1	29.6	37.5	June 28	27.7	38.3
September 2	29.3	37.7	July 27	29.4	33.7
September 3	30.1	38.0	August 27	27.2	37.4
September 4	30.3	38.4	August 28	27.6	37.7
September 5	29.8	37.9	October 18	22.0	31.2
September 6	29.7	37.9	November 8	21.6	33.3
September 7	29.6	37.8			

Embryology and Life History

Several camera lucida drawings were made of the larvae of *O. equestris* while they were in the gill chambers (Figs. 4–7). No drawings were made of *C. virginica*, because this species is adequately treated in the literature and its life history is well known. The life history of *O. equestris* has been studied only by Gutsell (1926). The writer made additional observations on the time of spawning and on the attachment of larvae to culch material.

The sex of individual oysters was determined by means of the smear technique. Gonad tissues were also studied on permanent slides stained with haematoxylin and eosin. A total of 539 *O. equestris* were examined by the smear technique. These ranged

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PLATE II

FIG. 4. Camera lucida drawing of morula, taken from mantle cavity of *O. equestris*. *mac.*, macromere; *mic.*, micromere; *po. bo.*, polar bodies.

FIG. 5. Camera lucida drawing of blastula, taken from mantle cavity of *O. equestris*. *bl.*, blastocoele.

FIG. 6. Camera lucida drawing of veliger (lateral view), taken from mantle cavity of *O. equestris*. *an.*, anus; *di. gl.*, digestive gland; *mo.*, mouth; *mu.*, muscle (posterior); *st.*, stomach; *ve.*, velum.

FIG. 7. Camera lucida drawing of later veliger (ventral view) than Figure 6, taken from mantle cavity of *O. equestris*.

FIG. 8. Camera lucida drawings of the prodissoconch shells of *C. virginica*, *O. equestris* and *O. frons*. (Drawn by S. H. Hopkins.)

PLATE II

FIG. 4

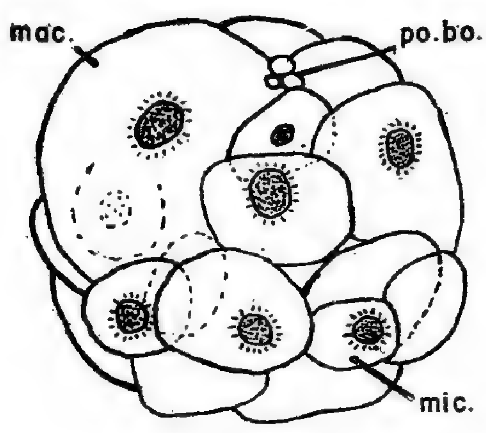
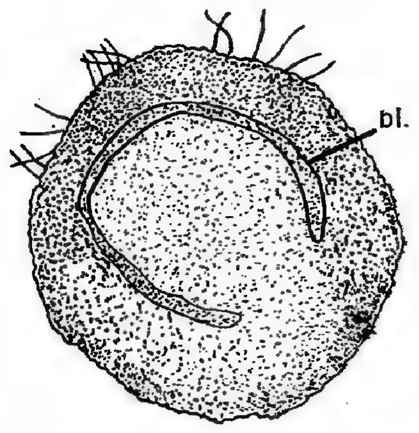

mac.
po.bo.
mic.

FIG. 5



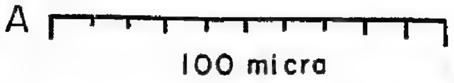


FIG. 6

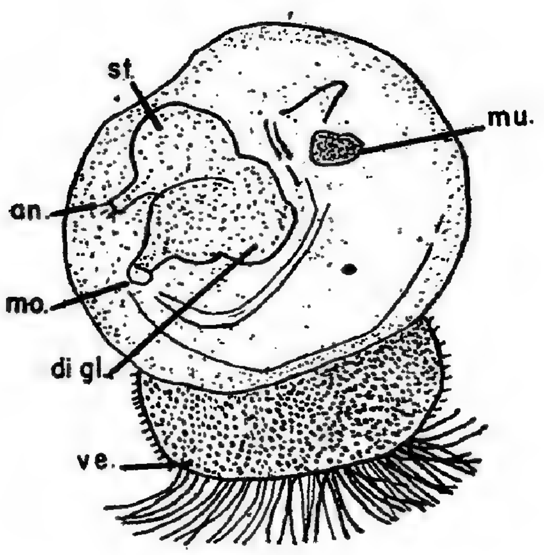

st.
mu.
an.
mo.
di gl.
ve.

FIG. 7

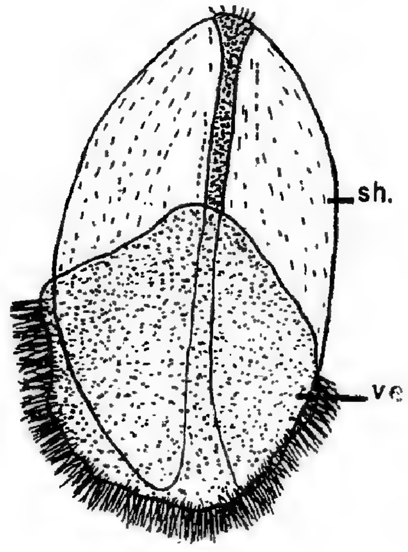
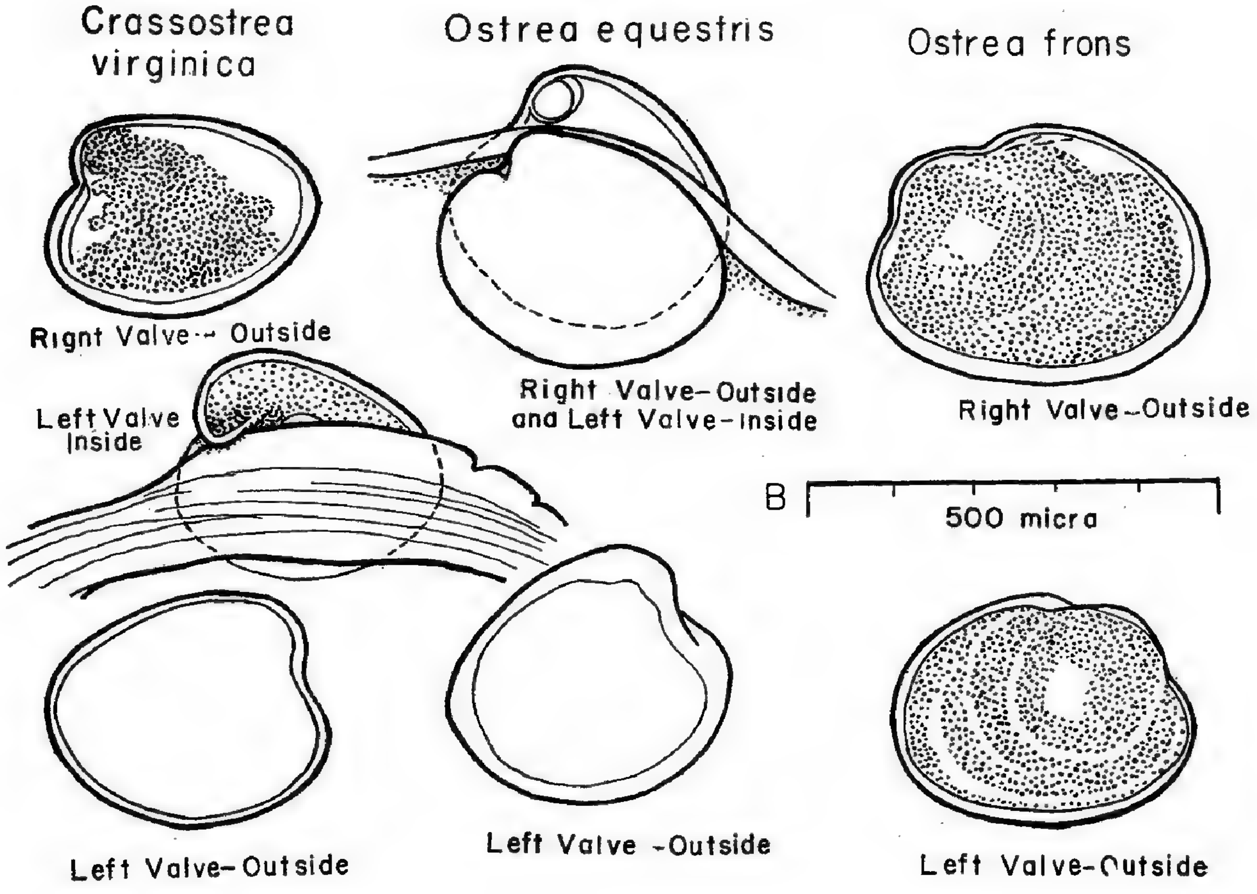


FIG. 8


Crassostrea virginica

Ostrea equestris

Ostrea frons

Right Valve – Outside

Left Valve Inside

Right Valve–Outside and Left Valve–Inside

Right Valve–Outside

Left Valve–Outside

Left Valve –Outside

Left Valve–Outside

from 4.0 mm. to 31.0 mm. in shell length. The majority of the examinations were made on oysters collected during the summer of 1951. Approximately half of the oysters were of known maximum age, since they had attached to culch planted at a known date. The age of the others was estimated from shell size (which was measured in all cases), and from the type of culch to which they were attached.

Anatomy

The anatomy of both genera of oysters is so well known that it is unnecessary to describe it again. However, a camera lucida drawing of a newly attached spat of *O. equestris* (Fig. 12) is included for comparison with the drawing of a small *C. virginica* (Fig. 13). Camera lucida drawings (Figs. 14–25) were made of the various organs that are concerned with the physiological functions that were investigated, such as feeding, defecation, and muscle contraction. These drawings were made from living oysters and from prepared slides.

Attachment of Larval Oysters

Studies on the attachment of the two species at Port Aransas involved several types of culch material. No attempt was made to determine the best period of attachment or the best type of culch as is usually done when the investigator is interested in commercial considerations. The investigation did include a study of the stratification of *Crassostrea*, represented by *C. virginica*, and *Ostrea*, represented by *O. equestris* and *O. frons*.

The main culch experiments at Port Aransas involved two series of observations, which extended from June 6, 1951 to November 8, 1952. Clean weather-bleached shells of *C. virginica*, measuring from about 90 to 125 mm. in length, were used as culch material. Holes 3 mm. in diameter were bored in the shells. Two shells were wired at one-half meter intervals, starting at the bottom, to a chain suspended in water of three and a half meters depth. A weight was placed on the bottom of the chain so that it would remain taut and the shells would retain their proper level in the rather strong current (Fig. 2).

The culch chain was examined at approximately monthly intervals during the summer months, and three times (October 21, 1951, December 30, 1951, and March 22, 1952) during the period from October, 1951 to May, 1952. At each examination, one of the two shells at each level was removed and two additional shells were attached. Also at each examination (after the first), the remaining shell at each level (which had been down for two periods) was examined. Therefore, the observations included in "Series A" were made on culch that had been in the water one month (longer during the winter months), and the observations in "Series B" were made on culch that had been in the water two months or longer. At first duplicate shells were put down in Series A, and there were fourteen examinations in this series and eleven in Series B.

All shells were examined under magnification and the numbers of spat of each species were determined for each level. At the same time, either all or a representative part of the oysters were measured to the nearest 0.5 mm. with vernier calipers.

The majority of the spat were less than 5 or 10 mm. in shell size when examined, and the species could not be identified by the adult shell characteristics. The spat were examined at magnifications of 10X to 50X. It was found that the prodissoconch shell afforded a reliable means of identification of the two genera, as reported by Ranson (1948). By means of camera lucida drawings of the three species (Fig. 8), it was found that they could be readily distinguished (Menzel, 1953). Other criteria for separating the two species that occur at Port Aransas are given below.

The effect of competing sessile organisms received attention also. Qualitative and quantitative counts were made of such organisms as hooked mussels, barnacles, serpulid worms, and sea squirts (numbers and sizes), and hydroids and encrusting and arborescent bryozoans (estimation of percentage of surface covered). No detailed analyses of these examinations are given here, but the effects of foulants on the attachment of oysters are discussed.

The culch material from Pensacola, Florida, consisted of asbestos plates 30 inches long and 4 inches wide, pitted on one side and smooth on the other. These had been held in a ladder-like holder with plates at one foot intervals from one foot above the bottom up to the surface, in water nine feet deep. The pitted side of the plate had been down, and the smooth side up. Because the surface plate had received no strike, it was not examined. There were two series of plates; the first had been in the water from May 27 to June 6, 1952, and the second from June 6 to June 10, 1952.

Each plate was marked off in ten blocks 5 cm. square, and two of these blocks selected at random (Snedecor, 1946, Table 1.2, pp. 10–13, was used) were examined on each surface. By means of the prodissoconch shell, all spat were distinguished as to species, except those on the top surfaces of the first series. These had been so crushed that the species could not be determined with any degree of accuracy from the prodissoconch shells. Therefore, 200 square cm. of area was examined for each plate, and the species were distinguished on 150 square cm. with one exception. The plate six feet above the bottom in the second series had been lost, so that the species were distinguished on an area of only 50 square cm. for this level. On one plate all the blocks were counted on one surface, and a chi square analysis was made to ascertain that the samples were representative.

In addition, several observations were made at various levels on the rocks (Fig. 1) that extend out from the jetty at Port Aransas to determine whether there was a difference in stratification of naturally occurring *O. equestris* and *C. virginica.* Random plankton tows were also made at different levels, and the species of late umbo larvae were determined.

Growth Studies

It was noted early in the investigation that *C. virginica* reached a much larger shell size than did *O. equestris.* Studies were performed to compare the shell growth of the two species. Oysters used were of known maximum age, *i.e.*, they were attached to culch planted on a known date.

Experiments I, II and III contained oysters of both species which had attached to oyster shell culch. All spat except the larger ones were culled from the culch. The remaining spat were measured with vernier calipers to the nearest 0.5 mm. in length (from umbo to posterior end of right shell) and height (greatest dorso-ventral distance). These oysters were numbered, and the location of each on the culch shell (inside or outside surface, and the position with respect to the umbo and adductor muscle scar) was noted so that records of the measurements could be kept on each oyster separately. The oysters were placed in wire cages, of one-half-inch mesh hardware cloth, about one foot square and from eight to ten inches high. These were suspended from beneath the laboratory in water four meters deep. One cage was suspended one-half meter from the bottom in all three experiments, and one was also suspended three and a half meters from the bottom in Experiment II. In all of the experiments there were several more oysters at the start than at the end. Only the measurements of those individuals which survived to the end of the experiments were included in the averages.

On each examination all adhering organisms were removed and the silt was scrubbed off. During the summer months especially, many sessile animals, such as barnacles, hydroids, bryozoans, and other oysters, were attached to the experimental oysters. The removal of these was more time-consuming than the actual measurements. The original plan was to make monthly examinations, but this was not possible after the summer of 1951.

Experiments IV and V included only *O. equestris,* which were attached to glass slides suspended one-half meter from the bottom in water of two meters depth. After measurements, the slides were replaced in the wooden frames (*vide* physiological observations) at the same depth. One frame was suspended one-half meter from the bottom, the other one and one-half meters from the bottom. The slides were carefully cleaned and culled so that each oyster was separate. They were numbered with Roman numerals and each oyster was numbered with an Arabic numeral. The majority of the spat had attached to the undersides of the slides, which had been planted parallel to the bottom, and they were replanted in the same position. In these experiments the thickness of the shell was measured (as well as the length and height) by subtracting the thickness of the slide from the total thickness of the slide and oyster.

The data were analyzed mainly by calculation of the percentage of increase for a comparison between the two species. A regression line was also calculated. In order to have one unit for comparison, an Index was computed. Index I was the product of length and height; Index II, the product of length, height and thickness (Experiments IV and V).

Predators, Diseases and Mortality

The literature on predators and diseases known to occur at Port Aransas was surveyed. An evaluation was made from this survey and from observations recorded during the course of the experiments.

Field observations were made on some of the enemies of oysters which occur in this region. A notation was made of the cause of death of all the experimental oysters if it could be determined. Similar notes were made on dead oysters observed in the field.

Originally ten growth experiments were started, but data from only five are presented. Various accidents befell the experiments in this unprotected location, which was subject to wave action from storms as well as from passing ships in the channel, so that the data from five of the experiments were only fragmentary. Also, because these experiments included only one of the two species, no comparisons could be made. However, mortality data from all of the experiments were used.

Feeding Observations

Observations of the feeding of the two genera of oysters were made by use of the so-called "glass oyster" (Burkenroad, 1953).

Ryder (1883) observed small *C. virginica* in the living condition under the microscope and gave some description of the ciliary movement. Nelson (1923a, b), Hopkins (1934b, 1936a, b, d) and others studied small oysters that had attached to glass slides and plates, but their observations, made under magnification, were through the right or free valve. Dr. E. J. Lund, formerly Director of the Institute of Marine Science, made some preliminary observations through the left valve of *C. virginica* attached to glass. Mr. Martin Burkenroad of this institution found that small oysters could be seen better, and oysters of a larger size could be observed, if they were viewed through the left valve. He used a dissecting microscope to study oysters attached to the inside of glass jars. Mr. Burkenroad explained his technique and urged that more observations be made. The writer made some refinements in the techniques used by previous investigators.

Microscope slides 75 mm. long, 25 mm. wide, and 1 mm. thick were used for the majority of the observations. These slides were immersed in the water for a period of time, and the oysters of both species attached to them. The slides were enclosed in a wooden box (Fig. 3) and suspended at two levels, near the bottom and near the surface, in water of two to four meters depth.

The slides were removed from the boxes and cleaned of all foreign particles by light washing, so as not to injure the attached spat. The majority of the observations were made on spat under 5 or 6 mm. long, but it was found that it was possible to observe *C. virginica* up to about 15 mm. and *O. equestris* up to about 10 mm. in length. The slides were placed parallel to the bottom, and usually there were no spat on the upper side. The upper side was cleaned thoroughly, and then the slides were immersed in shallow halves of Petri dishes so that the upper side was up. Thus when viewed through the microscope, the oyster was seen through the slide with the left valve next to the objective of the microscope. Because of the slide thickness, it was not possible to utilize the higher power of the compound microscope in such an arrangement. Usually the magnification was approximately 100X. On several occasions cover glasses (0.15–0.17 mm. thick), which made it possible to use magnifications up to 880X, were used as culch.

When slides were being studied, they were placed so that they were raised from 10 to 15 mm. above the bottom of the dish in order to allow free movement of the free right valve. It was found that there was less diffraction of light if the water level was deep enough to cover the slide about 0.2 mm. In the case of the cover slips, they were cleaned on one side and then placed with the oyster side down over Syracuse watch glasses filled with sea water.

During the summer of 1951, when the observations were being made at Port Aransas, the slides were kept suspended in the water until they were used. During 1952, the slides, with the attached spat, were wrapped in paper toweling wet with sea water and brought to College Station. The oysters were out of water about six hours before being placed in finger bowls of sea water at College Station. The bowls were placed in a cold room where the temperature was maintained at 6–9° C to lower the metabolism. On one occasion when the air temperature was very high (August) there was considerable mortality, but at other times the oysters, when examined the next day, appeared to be normal.

Several types of particles were presented to the oysters in the feeding observations. This was done by gently introducing a sea water suspension of the particles into the dish by means of a pipette drawn out to an opening of about 1 mm. or less in diameter. The following types of particles were introduced:

1. Plankton
   a. From net tows.
   b. From "settlings" in an enameled bucket of sea water drawn from the laboratory dock (containing the larger phyto- and zooplankton and detritus).
   c. Stained with neutral red and washed several times in sea water.
2. Finely pulverized algae (*Ulva* sp.).
3. Carmine particles.
4. Charcoal.
5. Haemoglobin.
6. Fine carborundum.

Other Physiological Observations

The technique of using living oysters with both valves intact and *in situ* afforded an opportunity to observe other activities besides feeding. The majority of these observations were incidental to the primary purpose, which was to compare ingestion of food in the two species.

The passage of particles into and along the digestive tract was observed and timed by the use of carmine and stained plankton. The contraction of the mantle, palps, gills, and adductor muscle, and the ciliary action on the mantle, gills, palps, and digestive tract were studied in connection with the feeding observations.

In August, 1952, an apparatus was made by which the temperature in the dish containing the slide with the small oyster attached could be lowered at a rate of one-tenth of a degree Centigrade per minute. A hole was bored in the side of a Petri dish and a Weston metal thermometer was inserted. The dish was placed over a coil of copper tubing leading from a carbon dioxide tank. The coil was so made that it fitted over the stage of a microscope and a valve was placed near the coil. The lowering of the temperature could be controlled by regulating the amount of escaping gas. By placing the entire coil and dish in an insulated box, the temperature could be lowered to 0° C. Since the apparatus was perfected after the setting season was nearly past, few observations were made with it. The effect of low temperature on heart beat, ciliary action, and muscle contraction was observed. These preliminary studies are discussed below in the appropriate sections.

EMBRYOLOGY AND LIFE HISTORY

Introduction

The embryology and life history of the two genera of oysters are well known, and no attempt is made here to review the entire field, but a partial review of some of the literature is given and some observations on *O. equestris* are described.

Crassostrea

The embryology of *C. virginica* was described by Brooks (1880, 1905), who fertilized the eggs *in vitro* and made drawings of various stages of the developing larvae. These studies have been supplemented by those of J. Nelson (1902, 1903), Ryder (1884) and Stafford (1905, 1909, 1910, 1913). *C. virginica* spawns when the temperature of the water reaches 18–25° C. The more southern the habitat, the higher the critical temperature for spawning (Nelson, 1928). Fertilization is external; within several hours a swimming embryo develops, and after about 30 hours the straightline stage is reached. Continued growth and development lead to the so-called "umbo-stage". This occurs within 8 or 10 days after spawning. Just before attaching to some suitable material, called culch, the umbo-stage develops a pigmented spot and is then called the "eyed" stage.

The developmental stages of *C. gigas* (Thunberg), the Pacific oyster, have been investigated by Amemiya (1928), Fujita (1930, 1934), and Hori (1926). Roughley (1933) studied the Australian oyster, *C. commercialis* Iredale and Roughley. Amemiya (1926) has studied *C. angulata* (Lamarck), the Portuguese oyster.

Burkenroad (1931a), Coe (1932b, 1934, 1936a, b, 1938), A. B. Needler (1932), Galtsoff (1937), Menzel (1951), and others have investigated the change in sex of *C. virginica.* This species is predominantly protandric; the first sex to develop is usually male, and the percentage of females increases as the oysters age. Females may revert to males, however, and Coe (1936a) and Menzel (1951) found that some young oysters may first develop as functional females and later change to males. But there is no alternating rhythm of change in sex such as is found in *O. edulis* and *O. lurida* (which are reported to be strictly protandric).

Ostrea

The anatomy of the larval stages of *O. edulis* and the other species of *Ostrea* is similar to that of *Crassostrea.* Cole (1937, 1938) discussed the metamorphosis of the larva of *O. edulis* at the time of its attachment. Korringa (1941) reviews all the previous literature on the life history of *O. edulis* and gives his own observations on the behavior before and during attachment.

Orton (1928) states that the genus *Ostrea* is found mainly in cold water. Korringa (1941) says that *O. edulis* can spawn when the temperature is 15–16° C., but will have the most successful spatfall when the temperature has risen to 18° C. The fertilized egg is retained in the gill chambers until an advanced stage of development. The releasing of the larvae into the water is called swarming, and the stage of development at which they are released may vary. Korringa (1941) says that the size of the larvae when released ranges from 165 to 200 micra and that the mature larvae range from 275 to 285 micra. After swarming, the larvae are pelagic for several days before they attach. Stafford (1914) estimated the period during which the larvae are in the branchial chamber in *O. lurida* Carpenter to be about sixteen days in the northern waters. Coe (1931a, b, 1932a) studied this species in California and found the period to be from ten to twelve days in the warmer waters.

There have been many descriptions of the alternation of sex in *O. edulis.* Orton (1921, 1922, 1924, 1927a,b, 1933) and Orton and Amigthaligan (1931) made a series of investigations on this phenomenon. Korringa (1941) summarized all the previous work dealing with sex reversal. Cole (1942) gives the results of his own work as well as a summary of previous work. He found that *O. edulis* may become sexually mature (as males) before they are one year old if grown under the most favorable conditions, but they usually do not reach sexual maturity until their second summer. The female phase follows, and oocytes develop in the follicles while spermatogenesis proceeds in the lumen. All oysters one year old or older change sex at least once and usually twice each summer; those which start the summer as males later change to females and still later revert to the male condition, all in one season. Coe (1931a,b, 1932a,e) found that *O. lurida* in California is regularly protandric and that it spawns at least seven months of the year in those waters. This species may reach sexual maturity twenty to thirty weeks after attachment, and thus may have two generations a year.

TABLE II

Sexual Condition of Ostrea equestris: Number in Each Condition

Age (days)	5–21	22–30	31–60	60–125	Over 125	
Size Range (mm.)	**3–6**	**5–10**	**8–10**	**12–25**	**15–30**	**Total**
Males	0	66	201	87	47	401
Females	0	1	22	18	13	54
Sperm and Eggs	0	0	3	0	1	4
Sperm and Larvae	0	0	3	4	2	9
Sperm, Eggs and Larvae	0	0	0	1	0	1
No Development	36	9	4	13	8	70

TABLE III

Sexual Condition of Ostrea equestris: Percentage in Each Condition

Age (days)	5–21	22–30	31–60	60–125	Over 125	Total
Males	0.0	86.8	86.3	70.7	66.2	74.4
Females	0.0	1.3	9.4	14.6	18.3	10.0
Sperm and Eggs	0.0	0.0	1.3	0.0	1.4	0.7
Sperm and Larvae	0.0	0.0	1.3	3.3	2.8	1.7
Sperm, Eggs and Larvae	0.0	0.0	0.0	1.0	0.0	0.2
No Development	100.0	11.8	1.7	10.5	11.2	13.0

Ostrea equestris

Gutsell (1926) examined specimens of *O. equestris* attached to scallops at Beaufort, North Carolina. He found that they were alternating hermaphrodites, similar to *O. edulis.*

During the present investigation a total of 539 individuals of *O. equestris,* collected at Port Aransas, were examined for sex by the smear technique. Some oysters were later sectioned and permanent slides made. The data are given in Tables II and III. It was found that 10% of the total number could be identified as female. However, of the 54 females in the sample, only 45, or 83.4%, contained eggs; the other 9 had no distinguishable gametes, but did have larvae in the gill chambers. The majority of the oysters examined (74.4%) were males. Of these, 85% were considered sexually functional at the time of examination, because the sperm balls were motile (Fig 14). The other 15% had immotile sperm balls. Nearly 1% (0.7%) contained both eggs and sperm. In all such cases the ova appeared immature and there were few sperm balls. A larger number of individuals had both motile sperm balls and larvae in the gill chambers. One of the sectioned oysters had a few eggs, many sperm balls, and also larvae. Seventy oysters (13.0%) had no developed gametes. Over half of these were under three weeks of maximum age (and under 6 mm. in shell length), but one-third were over two months old.

Aside from the 70 oysters which were too young to show any gonadal development, there were 469 oysters in which sex products were identified; of these, 85.5% were males, 11.5% were females, and 3% were transitional between sexes. Of the latter (14 individuals), 5 were changing from male to female and 9 were changing from female to male.

The smallest male oyster seen was 5.5 mm. long and 5.0 mm. high. This oyster, examined June 28, 1952, was attached to culch planted June 2, 1952. The sperm balls were motile. The smallest female, examined July 9, 1951, was 8.5 mm. long and 8.0 mm. high, and had attached to culch planted June 6, 1951. The ova seemed mature. Only six of the females were under 10 mm. long, and all except the one mentioned above were over one month old.

It would have been desirable to examine more oysters in each size group at regular and frequent intervals through the year. But even this preliminary study supports Gutsell's (1926) conclusion that *O. equestris* is an alternating hermaphrodite, and is similar in that respect to *O. edulis* and *O. lurida.* Three sexual phases occur in the first season in *O. equestris* as Coe (1931b) found for *O. lurida,* but whether there are more than three phases during the first season is not known.

The data indicate that young oysters may develop sperm as early as 26 days after attachment and ova within 33 days, although the average oyster reaches maturity at a much later age. Menzel (1951) had found that *C. virginica* can become sexually mature in 28 days, and Paul (1942) found that *C. madrasensis* Preston attained sexual maturity in 21 days. There is a possibility that *O. equestris* may sometimes develop as a female in the first phase, since one female was found that was only 33 days old. But from the other data it seems that this species is predominantly protandric like the other species of Ostrea. A study of individuals containing gametes or larvae indicates that the change from female to male is more rapid than the reverse change; specimens were found with immotile sperm balls and mature eggs or larvae, but none with mature sperm and immature eggs.

O. equestris set when the water was about 20° C. or below in the spring, and setting continued in the fall to a temperature below 20° C. (see Table I and the culch data). *C. virginica,* on the other hand, did not start attachment until the water temperature had risen to about 25° C. in the spring, and setting ceased after the temperature had dopped below about 25° C. in the fall (see Table I and data on culch material).

A few of the larval stages, taken from the branchial chambers, are shown in Figures 4–7. Several attempts were made to fertilize *O. equestris* eggs *in vitro* in order to obtain the young stages. These efforts never met with any success. Amemiya (1926) reported that he was unable to fertilize *O. edulis* eggs *in vitro,* although it has been found that it is easy to do so with *C. virginica* eggs.

ANATOMY

Introduction

The anatomy of oysters has been the subject of many studies. Several textbooks of invertebrate zoology describe or illustrate the anatomy of an oyster. There have been many detailed accounts of the anatomy of some of the structures such as the gills, mantle and stomach. Among these are the studies by Kellogg (1892), Ryder (1884), Yonge (1926), Awati and Rai (1931), Elsey (1935), and Nelson (1938). Although several hundred permanent slides were made during the present study, and some whole specimens were cleared for anatomical study, the writer has chosen not to give another detailed description of the entire anatomy. Attention was centered on two points: first, comparison of some structures of the two species, especially those structures concerned with feeding; and second, the anatomy of the shell (in connection with the observations made on the "glass" oyster).

The following description is taken mainly from Awati and Rai (1931), Borradaile and Potts (1935), Parker and Haswell (1940), Moore, Lalicker and Fischer (1952) and Shrock and Twenhofel (1953). This description is only general, and a few of the structures will be discussed in more detail later.

Adult oysters are considered to be monomyarian mollusks (Plate IV), although the mature larvae possess two adductor muscles. (The anterior adductor muscle has been seen on several occasions in adult *C. virginica.*) The two valves are not mirror images, and attachment is always by the left valve. The soft parts inside the shell are enclosed by the two-lobed mantle, which secretes the shell. The mantle is of an open type; the lobes are joined only anteriorly and along the mid-longitudinal lines, and are open in the posterodorsad and posteroventrad regions. Although there are incurrent and excurrent regions, there are no incurrent nor excurrent siphons as such.

The anterior end is considered to be at the hinge ligament of the umbo (Nelson, 1938). The hinge ligament is composed of elastic conchiolin material. When the shells are closed by the contraction of the adductor muscle, the hinge ligament is stretched. Its elasticity causes the valves to open again whenever the muscle relaxes. The mantle or pallial lobes are attached to the visceral mass anterior to the mouth. The mantle and the two pairs of labial palps, which surround the mouth and are adjacent and anterior to the gills, form a sort of hood in the oral region. The mantle lobes are joined along the mid-longitudinal line and form two chambers in the mantle cavity. In the ventral chamber, called the branchial (epibranchial) or inhalent chamber, are found the two pairs of lamellae, forming two gills. The upper chamber is called the suprabranchial or exhalent chamber (the posterior-dorsal part is often called the cloacal chamber). An esophagus leads from the mouth dorsad to the stomach, in the anterior part of the visceral mass. Surrounding the stomach are the digestive glands, and to the outside of these are the gonads, which extend posteriorly to the pericardial chamber. The intestine leads to the anus after making one or more loops in the posterior visceral mass.

The anus empties into the exhalent chamber just posteriad and dorsad to the adductor muscle, which is more or less centrally located (more posteriorly in *Crassostrea*). Between the posterior part of the visceral mass and the adductor muscle lies the pericardial chamber, in which is found the heart. The heart is composed of a single ventricle and two auricles fused into a single chamber. The intestine passes dorsally through the pericardial chamber. Figure 12 is a camera lucida drawing of a small *O. equestris* and Figure 13 is a cemera lucida drawing of a small *C. virginica.* The lamellae of the gills are not yet developed into the adult condition, but the figure shows the parts mentioned above.

Crassostrea (called *Gryphaea*) and *Ostrea* have been separated by Ranson (1939, 1948) on the basis of the prodissoconch shell. Nelson (1938) had found that *Crassostrea* contained a promyal chamber while *Ostrea* did not.

Adult oysters lack the foot which is found in most pelecypods, although it is present in the later larval stages. Adult oysters have two pair of ganglia, the cerebral and visceral. Cole (1938) found that the pedal ganglia are present in the larva and may be distinguished for 24 hours after attachment. Ranson (1936) shows pedal commissures in adult oysters.

Shells

The shells of mollusks are composed of three layers. The outermost is called the periostracum and is composed of conchiolin. The middle layer beneath the periostracum is the prismatic layer, composed mainly of prisms of calcium carbonate in the form called calcite. The inner layer, the nacre or mother of pearl, is calcium carbonate in the form of plates called aragonite (Pelseneer 1906, Cooke 1895, Shrock and Twenhofel 1953). According to Bull (1927), the main chemical composition of the shell is calcium carbonate with traces of calcium phosphate and some other materials. The periostracum or conchiolin is a horny, nitrogenous substance.

Orton and Amigthaligan (1927) (confirmed by the present investigation) found that in the oyster conchiolin could be laid down on the inner surface of the shell by the mantle and covered by limy deposits so that the layers are not in their usual order.

The right and left valves of both species were treated with hydrochloric acid and the conchiolin remains were examined under magnification. The conchiolin of the right valve appeared "cellular," whereas that of the left valve was more membranous, like a thin plastic sheet, and fairly transparent. The remains of both valves were light olive brown in color, even after several washings in water. The conchiolin appeared to be thicker in the right valve, but this may have been due to the fact that it was less translucent because of the "cellular" structure. Slides made of attached spat showed that the conchiolin material, which remained after decalcification, took no stain (haematoxylin, eosin, acid fuchsin or alum cochineal).

Upon first examination, the smaller specimens of *C. virginica* and *O. equestris* (under 10 mm. long) appear similar in external features. Superficially the larger specimens look alike also, but they can be distinguished after a little experience. Generally *O. equestris* is rounder than *C. virginica* (growth experiments substantiate this statement), but this is not a very good criterion because some of the smaller specimens of *C. virginica* are round, and some of the larger specimens of *O. equestris* are much longer than wide, especially if they are growing in a crowded position. Any oyster over about 35 mm. in length at Port Aransas was likely to be *C. virginica.* In more nearly oceanic waters *O. equestris* grows larger than this. Gunter (1951b) found *O. equestris* up to 72 mm., and some specimens were seen by the writer from the Gulf of Mexico off Padre Island (Texas) and some from North Carolina that measured up to 50 mm. in shell length. However, these larger *O. equestris* have a growth habit in relation to the culch which is different from that of *C. virginica. O. equestris* will often be attached for almost the entire shell length, and when the posterior edge leaves the culch the left valve is at almost right angles to the right valve. This species is much thicker in proportion to the length than *C. virginica.* The left valve of *O. equestris* is not so deep-cupped as that of *C. virginica.*

The two species can be distinguished with certainty by the presence or absence of denticles inside the margins of the valves (see frontispiece). *O. equestris* possesses these, and *C. virginica* does not. The presence or absence of denticles was used at first for species identification and later to check on doubtful determinations when other characteristics were being employed. The denticles are on the margins of the right valve of *O. equestris,* with corresponding indentations on the left valve. In the smaller oysters the denticles were seen only near the umbo, and the lowest number ever seen was two; i.e., one denticle and one indentation dorsad and one of each ventrad to the umbo. In larger oysters, over 15 mm. in shell length and over six months in age, the denticles often extend completely around the free circumference of the shell. From casual observations, it seemed that the progressive increase from the umbo was as rapid on the dorsal as on the ventral margin of the shell.

It was found that *C. virginica* could be distinguished from *O. equestris* after a size of from 3 to 5 mm. had been reached by the appearance of a "chalky" streak on the right valve in *C. virginica.* The chalky streak extended from the umbo to the posterior periphery of the shell, becoming wider and more diffuse posteriorly. This chalky streak was recognized by Mrs. Ruth Ellis Allen when she made detailed drawings of spat on culch material in the Chesapeake Bay area for a Virginia Fisheries Laboratory publication (Newcombe and Menzel, 1945). Although no significance was placed on this feature at the time, it was found in the present investigation that it was an easy and reliable means of distinguishing the species. The two species were separated by this means in a sample of several hundred oysters and afterward the identification was checked by opening the shells and looking for denticles. The identifications were found to be more than 98% accurate. The few errors that were made were in the smaller (younger) specimens, before the chalky streak appeared in *C. virginica* (Fig. 13). The chalky streak is less translucent than the surrounding shell, and gives the appearance of a raised ridge. But careful examinations at various angles revealed that the ridge was an optical illusion.

Ryder (1883) correlated the pigmentation of the soft parts, especially the adductor muscle, with that of the shell in *C. virginica.* Orton (1937), describing the shell of *O. edulis,* said that the left valve is almost always shiny brown in color and that the right valve may vary from a uniform dirty brown to one having streaks of pink and purple. It was thought in the present investigation that there might be some difference in the shell pigmentation of the two species studied. But pigmentation did not prove to be a reliable criterion for distinguishing the species. Usually there was heavy pigmentation in the shell of *O. equestris,* although it was seldom as intense as in *C. virginica.* There are purple stripes in the spat of both *C. virginica* and *O. equestris,* but they are usually less brilliant in the latter. About five per cent of the specimens of *O. equestris,* growing at various depths and under various conditions, had a light brown pigmentation in the entire shell. This condition was never seen in *C. virginica.* (No investigation of the pigment or its causes was made.)

The shells of spat of both species were transparent for a time after attachment, and seemed to be composed entirely of conchiolin and aragonite. Under a microscope, the soft parts of living spat could be seen through the shell; as long as the spat were small, the finest details could be seen quite clearly. As the oysters became older and larger, the shell became less transparent because of the deposition of chalky material (calcite). After a time the valves became so chalky that it was impossible to see through them. The chalky streak in *C. virginica* made the right valve less translucent from the start, but when the spat was viewed through the left valve, enough light was transmitted so that the soft parts could be seen. After a few days the left valve became chalky also. The chalky deposition in the right valve proceeded somewhat differently in the two species. In *C. virginica* it progressed both dorsad and ventrad from the chalky streak. In *O.*

equestris the chalky deposition spread, more or less uniformly, from the mid-anterior region and progressed posteriad and dorsoventrad in an irregular manner, but followed the shape of the rounded contour of the posterior part of the shell.

The chalky deposition in the left valve proceeded differently from that in the right valve. In both species, streaks of chalky calcification began on each side of the umbo and progressed around the margin of the shell both dorsally and ventrally. In the posterior region about level with the posterior margin of the adductor muscle (which is further posterior in *C. virginica* than in *O. equestris*) the streaks broadened and finally met. The chalky appearance then proceeded anteriorly, first covering the region of the shell over the adductor muscle and then the region over the pericardial chamber. At the same time the oysters were growing larger and the adductor muscle was moving posteriorly in proportion to the shell growth. Meanwhile the bands increased both dorsally and ventrally in the anterior region. This finally resulted in a more or less round space over the anterior visceral mass, which was the last portion of the shell to become chalky and to obscure the underlying soft parts. Chalky deposition proceeded much more slowly in the left valve than in the right, and the soft parts of some specimens of *C. virginica* up to 15 mm. long could be observed through this valve.

The muscle scar in *C. virginica* was pigmented (purplish black), whereas it was clear in *O. equestris* (Frontispiece). This conforms to the *Crassostrea* and *Ostrea* characteristics as discussed by Nelson (1938).

Mantle

Studies of the mantle have been made by Kellogg (1892), Awati and Rai (1931), Elsey (1935), Nelson (1938), and many others. The ciliary action on the mantle was investigated in the present study in connection with feeding reactions, and these data are discussed in that section.

Hopkins (1935b) showed that contraction of the tentacles regulated the flow of water. Nelson (1938) showed that the contraction of the tentacles regulated the passage of water with suspended particles in and out of the mantle chamber. He also discussed the contraction of the mantle into siphon-like structures (see under physiological observations.)

A tract of cilia was found on the right mantle that was specialized to transfer the pseudofaeces to the exterior of the shell in the exhalent region. These cilia beat in the opposite direction to the incoming flow of water. This tract of cilia is called here the pseudofaeces tract. It has been depicted previously in several other species of the two genera, including *C. commercialis* (Roughley, 1933) and *O. edulis* (Orton, 1937). The pseudofaeces tracts of *O. equestris* and *C. virginica* are shown in Figures 12–16.

It was found that the point of exit of the pseudofaeces was different in the two species: mid-ventral in *C. virginica* and more posteriorly in *O. equestris*. Previous investigators have figured the same relative exit point for the two respective genera. A more detailed discussion of the activity of the mantle is given in the section on physiological observations.

Nelson (1938) found only a diffuse pigmentation in the mantle of *O. edulis*, despite the fact that the oysters were in sunlight in open tanks less than 15 cm. deep. He also found dense pigmentation in *C. virginica* and *C. angulata*, and Schiedt (1904) induced pigmentation in the entire body of *C. virginica* by exposure of the animals to strong sunlight. The writer found that *O. equestris* did have pigment around the mantle border, but it was not so intense as in *C. virginica,* and pigmentation was fainter in oysters from deeper water than in those from locations where there was more light penetration.

Sections through the lobes of the mantle were examined to determine whether there was any histological difference which might account for the difference in the conchiolin of the two valves (see page 87), but none was found.

Gills

There are many descriptions of oyster gills in the literature previously cited. Nelson and Yonge (1947) give some information on the development of the gill of young *C. virginica.* They found that the mature pelagic larva has a single left demibranch consisting of eight paired, closely placed papillae. These pairs of papillae separate within six hours after attachment except at the tips, and form a V.

Figure 12 shows the immature gill seen in a very small oyster. One feature of the gills of *C. virginica,* not found in *O. equestris,* was the presence of bars or bands of pigment. The pigmented bars extended from the base of the gills ventrad to the free edges, and were first apparent in oysters about 2 mm. in shell length, in which one pigment bar was seen about level with the adductor muscle. As the spat grew older and larger, more such bars appeared. There were more bars posterior than anterior to the adductor muscle, and in oysters of about 10 mm. there were from six to ten such bars. It might be mentioned here that additional pigment appeared in other soft tissues as *C. virginica* became older and larger. Some of the pigment was correlated with the intensity of the sunlight to which the oysters were exposed. In those of 5 to 10 mm. size there appeared a pigmented area around the adductor muscle. The muscle scar on the shell itself became pigmented when a length of 10 to 15 mm. had been reached by the oyster. At these larger sizes, pigment extended over the pericardial chamber and visceral mass, and the basal portion of the gills was densely pigmented, especially if the oysters had been exposed to strong sunlight.

Palps

The palps have been shown in detail by Yonge (1926) and other investigators. The cilia on the palps and their activity are discussed below in the section on feeding. Figures 17 and 18 are camera lucida drawings of the palps of *O. equestris* and *C. virginica* in the living condition.

Digestive Tract

The esophagus, stomach, crystalline style and sac, and intestine have been described in detail by Yonge (1926), Awati and Rai (1931), Nelson (1938), and many others. As far as is known, the cilia-like structures on the tip of the rectum have not been described before. These were not found in specimens longer than about 8 mm., but were present in smaller oysters of both species. Their activity is discussed below in the section on feeding. Figures 19 and 20 are camera lucida drawings of these anal tufts of cilia-like structures.

Adductor Muscle

The adductor muscle is figured by several of the above-mentioned investigators, and Hopkins (1936d) discussed its structure when contracted and when relaxed. Figures 21 and 22 are camera lucida drawings of the contracted and relaxed positions.

Gonads

Orton (1921, 1922, 1924, 1927a,b, 1933), Orton and Amigthaligan (1931), and many others have studied sexual development in detail in *O. edulis.* Kellogg (1892) pictures the hermaphroditic condition in *C. virginica.* Coe, in a series of papers (1931a,b, 1932a,b,d,e, 1934, 1936a,b, 1938) has dealt with the anatomy as well as the physiology of sex change in *C. virginica* and *O. lurida.* Figure 23 is a camera lucida drawing of an hermaphroditic *O. equestris.* Figure 24 shows a sperm ball of *O. equestris.*

Circulatory System

Awati and Rai (1931) and many others have described the complete circulatory system. Figure 25 is a camera lucida drawing, made by the writer from life, of the accessory hearts discussed by Hopkins (1934a,b, and 1936a,b). These are found in the mantle.

ATTACHMENT OF LARVAL OYSTERS

Introduction

Obtaining a plentiful "strike" or setting of spat is one of the most important aspects of the oyster industry. This is true for all the species grown in the United States as well as for those in other countries. In the northern regions the obtaining of an adequate spatfall is one of the limiting factors in commercial oyster culture. On the South Atlantic and Gulf Coasts of the United States, where *Crassostrea virginica* is the only commercial species, oyster strike is usually abundant. As far north as North Carolina, and even in parts of Virginia, too much strike is more likely to cause trouble than too little (Menzel, 1953). In some places the spat attach so thickly that they must be separated or else the majority of the small oysters die and the remainder become misshapen (the so-called "coon" oysters). On one occasion, in Terrebonne Parish, Louisiana, the writer counted over 2000 newly attached spat on the inside surface of an oyster shell with an area of less than 60 square centimeters; this shell had been in the water for only one week.

In the saline waters along the Gulf Coast, one problem is caused by the fact that species of the genus *Ostrea* occur and set along with *C. virginica.* At Port Aransas, Texas, *O. equestris* occurs in considerable numbers, and farther east a second species, *O. frons,* occurs in addition to *O. equestris* and *C. virginica.* In the more saline regions, *C. virginica* is limited mainly to the intertidal zone. Here it occurs naturally on pilings, jetties and other structures, and in intertidal reefs. This limitation to the intertidal zone is due partly to the destructive action of the oyster conch (*Thais haemostoma* Conrad), the stone crab (*Menippe mercenaria* (Say)) and the sheepshead fish (*Archo-*

TABLE IV

Numbers of *O. equestris* (e) and *C. virginica* (v) That Attached at Each Level in Series A During Fourteen Periods, From June 5, 1951 to November 8, 1952.

Period	Dates		3.5 M.		3.0 M.		2.5 M.		2.0 M.		1.5 M.		1.0 M.		0.5 M.		Bottom	
	Planted	Examined	e	v	e	v	e	v	e	v	e	v	e	v	e	v	e	v
1	June 6, 1951	July 6, 1951	0	26	1	8	7	39	8	30	6	19	7	15	12	3	39	0
2	June 5, 1951	July 9, 1951	0	18	0	6	0	34	4	24	27	37	34	15	11	3	16	0
3	July 8, 1951	Aug. 5, 1951	0	10	1	7	0	12	0	13	5	7	4	2	44	1	8	4
4	July 25, 1951	Sept. 1, 1951	0	5	1	17	4	16	17	4	15	4	44	2	33	1	53	0
5	Sept. 1, 1951	Oct. 21, 1951	0	16	0	23	9	13	20	8	184	12	65	2	83	2	233	0
6	Oct. 21, 1951	Dec. 30, 1951	....	....	....	....	2	0	....	....	2	0	23	0	11	0	51	0
7	Dec. 30, 1951	March 22, 1952	....	....	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	March 22, 1952	May 11, 1952	1	0	6	0	13	0	16	0	1	0	7	0	6	0	1	0
9	May 11, 1952	June 2, 1952	0	41	1	34	11	29	15	12	33	2	107	0	99	11	150	0
10	June 2, 1952	June 28, 1952	0	17	....	....	0	6	4	10	13	14	31	19	91	8	62	0
11	June 28, 1952	July 27, 1952	0	11	2	17	2	31	4	11	9	7	40	4	95	4	121	0
12	July 27, 1952	Aug. 28, 1952	0	7	1	5	2	4	0	3	5	1	9	6	8	1	3	0
13	Aug. 28, 1952	Oct. 19, 1952	2	36	6	9	5	7	45	2	85	0	96	0	135	0	19	0
14	Oct. 19, 1952	Nov. 8, 1952	0	0	0	0	3	1	3	0	40	0	11	1	16	0	100	0

sargus probatocephalus Walbaum). *O. equestris* is found, often in considerable numbers, however, below the intertidal level at Port Aransas, Texas, and a third species, *O. frons,* occurred only on the lower levels on culch from Pensacola, Florida. These species are subject to the same depredations. On templates of an oil well platform off the Louisiana Coast, on which Gunter (1951a,b) found all three species growing, the zone of occurrence of the two species of *Ostrea* was lower than that of *C. virginica,* but overlapping.

The three species, thus, are found together, but the indications are that the genus *Ostrea* attaches at a much lower level in water of some depth whereas *C. virginica* occurs near the surface. This is in water of high salinity, approaching that of sea water; according to the writer's observations, *Ostrea* does not occur in waters of salinity below about 25‰. In order to compare the setting behavior of the different species, stratified culch experiments were conducted continuously at the Institute of Marine Science at Port Aransas, Texas. In addition, the writer examined two series of culch material from a somewhat similar experiment conducted by Dr. Philip Butler at Pensacola, in which a third species, *O. frons,* was also present.

The main purpose of the culch studies was to determine the stratification of the several species in their attachment. Along with the above, information was obtained on the approximate time of attachment,—*i.e.,* the duration of the setting season—and on the effect of fouling organisms. In addition, some observations were made on the stratification of *O. equestris* and *C. virginica* along the jetty at Port Aransas.

TABLE V

Average Numbers and Percentages of *O. equestris* and *C. virginica* That Attached at Each Level in Series A During all Periods From June 5, 1951 to November 8, 1952.

Levels	Numbers		Percentages	
	O. equestris	*C. virginica*	*O. equestris*	*C. virginica*
3.5 M.	0.3	20.8	0.1	22.7
3.0 M.	1.6	15.0	0.7	16.3
2.5 M.	4.1	20.9	2.2	26.5
2.0 M.	10.5	12.8	5.2	15.2
1.5 M.	30.4	7.7	16.2	9.8
1.0 M.	34.1	4.7	18.2	5.9
0.5 M.	46.1	2.4	24.6	3.1
Bottom	61.1	0.3	32.6	0.4

Studies on Stratification of Set of Oysters at Port Aransas

The results of the observations on set of oysters on stratified culch planted at half-meter intervals in water of three and one-half meters depth are given in Tables IV to XI and in Figures 9 and 10. Figures 9 and 10 are graphs of the percentages of *O. equestris* and *C. virginica* that attached at each level during all the periods of Series A and B respectively (Tables V and IX). The actual counts of each species are given in Tables IV and VIII (blank spaces indicate that the culch shells were lost), and Tables VI and X give the average number of spat of each species and the percentages that attached during each period. Tables VII and XI give the average numbers of spat on each culch shell per day at all the levels. The average number per shell per day was calculated for these tables because the periods were not of equal length.

The most striking feature of the results was the difference in the stratification of the two species. In both series, *O. equestris* spat were most numerous near the bottom and became progressively fewer toward the surface, whereas the opposite was true for *C. virginica.*

Tables V and IX and Figures 9 and 10 show the stratification of both species in both series of experimental culch. It is seen that a small number of spat of both *O. equestris* and *C. virginica* were found on the surface level and bottom level respectively in Series A, but in Series B no spat of *O. equestris* were seen on the surface shell during any of the periods, and the same was true for *C. virginica* on the bottom shell.

Spat of *O. equestris* were always found most abundantly on those shells on the bottom up to about a depth of 1.5 meters above the bottom for both series of culch (Tables IV and VII). The greatest break in numbers of spat of this species occurred between the 1.5 and 2 meter levels as shown by Tables V and IX and the figures. The numbers in the preceding tables are averages, and there were variations from these averages during the several periods, as would be expected (see Tables IV and VIII).

On the average, spat of *C. virginica* were found most abundantly at levels 2.5 meters (Series A) and 3.5 meters (Series B) from the bottom. As would be expected, there was variation from the average during the several periods. The sharpest break occurred between the levels of 2.0 and 1.5 meters above the bottom. It is interesting to note that the level 2.5 meters above the bottom had the largest average number of spat per shell in Series A but had less than the three upper levels in Series B.

TABLE VI

Average Numbers and Percentages of *O. equestris* and *C. virginica* That Attached at All Levels in Series A During Fourteen Periods, June 5, 1951 to November 8, 1952.

Periods	Numbers		Percentages	
	O. equestris	*C. virginica*	*O. equestris*	*C. virginica*
6/6/51–7/6/51	10.0	17.5	36.4	63.6
6/5/51–7/9/51	11.5	51.1	18.4	81.6
7/8/51–8/5/51	7.8	7.0	52.5	47.5
7/25/51–9/5/51	20.9	16.1	56.5	43.5
9/1/51–10/21/51	74.3	9.5	88.6	11.4
10/31/51–12/30/51	17.8	0.0	100.0	0.0
12/30/51–3/22/52	0.0	0.0	......	......
3/22/52–5/11/52	6.4	0.0	100.0	0.0
5/11/52–6/2/52	52.0	16.1	76.4	23.6
6/2/52–6/28/52	28.7	10.6	73.1	26.9
6/28/52–7/27/52	34.1	10.6	76.3	23.7
7/27/52–8/28/52	3.5	3.4	51.0	49.0
8/28/52–10/19/52	49.1	6.8	88.0	12.0
10/19/52–11/8/52	21.6	0.3	98.9	1.1
Average	24.5	10.3	70.4	29.6

The average number (as well as the total) of *O. equestris* on all shells at all levels was about three times greater than the average number of *C. virginica.* Over 70% of the spat in Series A and nearly 76% in Series B were *O. equestris* (Tables VI and X). Several factors may influence the greater numbers of *O. equestris* besides the fact that they were simply more numerous during the setting season. There may have been a better survival of *O. equestris* than of *C. virginica.* An analysis of the two series indicates this. On the average, there were only a little over 36% more spat per shell of both species on the culch in Series B than in Series A, despite the fact that the Series B culch had been in the water twice as long. Yet the Series B culch had almost 43% more *O. equestris,* but only a little less than 11% more *C. virginica* than the Series A culch.

Another factor that may have influenced the greater abundance of spat of *O. equestris* than of *C. virginica* is that the former species may have attached to old culch more readily. The culch near the bottom in the zone of greatest attachment of *O. equestris* and least of *C. virginica* was less fouled than that near the surface. A detailed analysis of the time of attachment from the size of the spat was impossible to make, but, from measurements made in both series, the general impression was that recently attached spat of *O. equestris* were more numerous than recently attached spat of *C. virginica.*

Still another factor may have been that *O. equestris* attached later in the fall and commenced earlier in the spring than did *C. virginica.* (There were two periods in Series A, Periods 6 and 8, Table IV, in which only *O. equestris* was found.) There were only two periods, however (Periods 1 and 2, Table VI), in which there was an average of more spat of *C. virginica* per shell at all the levels than of *O. equestris.*

The periods were too long to permit determination of the exact time that the attachment stopped in the fall or started in the spring. From a knowledge of the growth rate and from measurement of the spat at the time of examination, some tentative conclusions can be drawn. It may be seen from the tables, especially those for Series A, that *O. equestris* spat occurred during every period except the one from December 7, 1951, to March 22, 1952. *C. virginica* spat, on the other hand, were not present during the periods from October 21, 1951, until May 11, 1952, in Series A. In Series B, one *C. virginica* (and three *O. equestris*) were seen on the three shells that remained from the culch planted October 21, 1951, and examined March 22, 1952. The size of the one *C. virginica* spat indicated that it had attached shortly after the culch was planted. A general statement can be made that in 1951, *O. equestris* attached until about the first of November and *C. virginica* until about the middle of October. In 1952, *O. equestris* began to attach about the first of May and *C. virginica* about the middle of May. Table I gives the temperature of the water at these periods.

The experiments were not designed to measure the seasonal changes in intensity of spatfall; the culch was in the water too long for this, and the periods were not all of the same length. The numbers of spat counted were not the numbers that attached, but were those that set *and survived* during the period that the culch was in the water. In Tables VII and XI an attempt is made to get as nearly a true picture of the seasonal intensity of spat attachment as is possible from the data. In these tables, the average number of spat of each species that attached per shell per day at all levels during the several periods has been calculated. Table VII (Series A) gives a better picture of the seasonal intensity of setting for the two species than does Table IX (Series B), because the period in the water was approximately half as long. As survival is not such a large factor when the period in the water is shorter, the shorter period gives better data on setting intensity.

Table VII shows that the greatest intensity of attachment of *O. equestris* spat during 1951 was between September 1 and October 21. For a period of over 50 days, one would expect less spat per day than in shorter periods, but there was an average of nearly 1.5 spat per shell per day. The majority of these spat were small and probably attached in October. In 1952 the greatest intensity of setting was from May 11 to June 2, when there were 2.36 spat per shell per day on the average during a period of 22 days. The average per day continued high through the period ending July 27, but decreased after this date. It rose again in the period between August 8 and October 19, and was still higher on shells planted October 19 and examined November 8. Data in Table XI shows that in Series B the greatest numbers in 1951 were found on shells planted June 6 and examined

August 5, with very few after this. The second period, from July 25 to October 21, had very few spat, and it may be assumed that the majority of the spat seen in the first period attached in June and the early part of July. The large size of the spat when they were measured also indicates this. There were fairly numerous *C. virginica* spat on shells planted March 22 and examined June 2, 1952, and even more on those planted May 11 and examined June 28, 1952. Measurements of shell size indicate that the bulk of the spat on the culch of both series (A and B) had attached at about the same time—namely, in June. The data therefore indicate that the season of greatest attachment for *C. virginica* was in June. The setting decreased slightly in July, and more markedly in August, followed by an increase in the fall (about September). The fall strike did not approach the numbers that attached during June and July in either year.

TABLE VII

Average Numbers of *O. equestris* and *C. virginica* Per Shell Per Day That Attached at All Levels in Series A During Fourteen Periods, June 5, 1951 to November 8, 1952.

Period	*O. equestris*	*C. virginica*	Both species
6/6/51–7/6/51	0.33	0.58	0.91
6/5/51–7/9/51	0.34	0.50	0.84
7/8/51–8/5/51	0.28	0.25	0.53
7/25/51–9/5/51	0.55	0.16	0.71
9/1/51–10/21/51	1.46	0.19	1.65
10/21/51–12/30/51	0.25	0.00	0.25
12/30/51–3/22/52	0.00	0.00	0.00
3/22/52–5/11/52	0.13	0.00	0.13
5/11/52–6/2/52	2.36	0.73	3.09
6/2/52–6/28/52	1.10	0.41	1.51
6/28/52–7/27/52	1.17	0.37	1.54
7/27/52–8/28/52	0.11	0.11	0.22
8/28/52–10/19/52	0.95	0.13	1.08
10/19/52–11/8/52	1.08	0.02	1.10

Examination of Culch from Pensacola, Florida

Results of the examination of the culch from Pensacola, Florida are presented in Tables XII, XIII and XIV and in Figure 11. Table XII shows the results of the examination of the two sets of culch. Figure 11 is a graph of the percentage of each species that attached at each depth, pooling the figures from the two sets of culch. The depths in feet have been converted to the metric scale for comparison with Figures 9 and 10. The above graph was drawn from the data in Table XIV, which also shows the percentage of the total number of spat belonging to each of the three species, *O. frons*, *O. equestris* and *C. virginica*.

In Table XIII are given the results of counting all of the spat on an entire plate rather than on only a portion of the plate surface. Each 25 centimeter square block was counted separately and a chi-square analysis was made. The chi-square values show that the use of only a portion of the surface of a plate (the data given in Table XIII) was justified and that the portion counted was a statistically adequate sample. It was not the total number of oysters that was important in any case in the present study, but rather the stratification of the two genera.

Tables XII and XIV show that the stratification of *O. equestris* and *C. virginica* was about the same at Pensacola as at Port Aransas. The spat of *O. frons* showed the same

TABLE VIII

Numbers of *O. equestris* (e) and *C. virginica* (v) That Attached at Each Level in Series B During Eleven Periods, From June 6, 1951 to November 8, 1952.

Period	Dates		3.5 M.		3.0 M.		2.5 M.		2.0 M.		1.5 M.		1.0 M.		0.5 M.		Bottom	
	Planted	Examined	e	v	e	v	e	v	e	v	e	v	e	v	e	v	e	v
1	June 6, 1951	Aug. 5, 1951	0	13	2	12	11	20	15	18	26	22	45	2	102	0	41	0
2	July 25, 1951	Oct. 21, 1951	0	18	11	16	8	7	26	10	109	7	104	9	113	0	87	0
3	Sept. 1, 1951	Dec. 30, 1951	0	13	....	....	1	10	....	....	....	....	29	13	85	3	145	0
4	Oct. 21, 1951	March 22, 1952	....	....	....	....	0	1	....	....	0	0	....	....	3	0	....	....
5	Dec. 30, 1951	May 11, 1952	0	0	....	....	0	0	....	....	....	....	....	....	....	....	....	....
6	March 22, 1952	June 2, 1952	0	47	0	35	7	64	11	12	42	1	57	2	55	1	100	0
7	May 11, 1952	June 28, 1952	0	42	3	28	9	36	19	55	20	23	85	3	175	23	136	0
8	June 2, 1952	July 27, 1952	0	0	0	40	3	25	3	14	10	17	20	11	51	0	27	0
9	June 28, 1952	Aug. 28, 1952	0	19	2	11	2	6	5	9	21	3	73	0	63	0	51	0
10	July 27, 1952	Oct. 19, 1952	....	....	2	7	4	5	....	....	6	2	12	0	....	....	78	0
11	Aug. 28, 1952	Nov. 8, 1952	0	60	0	2	8	6	16	14	60	0	85	0	110	0	110	0

stratification of setting as that of *O. equestris. O. equestris* had a little steeper curve (as shown by Figure 11) at Pensacola than at Port Aransas; at Pensacola there were more spat at the lower depths and none above about 2 meters. The maximum numbers of *C. virginica* spat were found from about one to two meters above the bottom at Pensacola in water of less than three meters depth.[2] However, it should be noted that during the period that the culch was in the water, the salinity range was from 19.5 to 26.0 ‰. No culch was planted on the bottom, but it would be expected that the greatest numbers of *O. equestris* and *O. frons* and the least numbers of *C. virginica* would have occurred on the bottom, if the series of culch plates had extended all the way from surface to bottom.

TABLE IX

Average Numbers and Percentages of *O. equestris* and *C. virginica* That Attached at Each Level in Series B During all Periods From June 6, 1951 to November 8, 1952.

	Numbers		Percentages	
Levels	*O. equestris*	*C. virginica*	*O. equestris*	*C. virginica*
3.5 M.	0.0	23.6	0.0	25.2
3.0 M.	2.5	18.9	0.9	20.2
2.5 M.	4.8	16.4	1.7	17.5
2.0 M.	13.3	18.9	4.7	20.2
1.5 M.	32.7	8.3	11.7	9.8
1.0 M.	56.7	4.4	20.2	4.8
0.5 M.	84.1	3.0	30.0	3.2
Bottom	86.0	0.0	30.7	0.0

Discussion and Summary

The data show that *O. equestris* has a longer season of attachment than *C. virginica.* The setting season for *O. equestris* began approximately two weeks earlier in the spring, about the first of May when the temperature of the water was 20° C. or lower, and lasted approximately two weeks longer in the fall, until about the first of November when the temperature had decreased to nearly 20° C. The spawning activities of *C. virginica* were correlated with a water temperature of 25° C.

The total number of *O. equestris* spat on the experimental culch at Port Aransas was from two to three times the number of *C. virginica* spat. This may mean that *O. equestris* larvae were more numerous, or that they attached to the culch more readily, or that the spat had better survival than in *C. virginica,* or that their attachment was less affected by fouling of the culch. The fact that spat of *O. equestris* attached a month longer than of *C. virginica* accounts for some of the differences in numbers. *O. equestris* was concentrated in a narrower zone (near the bottom) than *C. virginica* (near the top), which would favor greater numbers of *C. virginica.* But the fact that the culch was usually less fouled near the bottom than near the surface would favor a greater number of *O. equestris* if fouling were an important factor. Detailed observations on fouling organisms are not presented here, but it may be said that fouling did not prevent abundant strike of both species at Port Aransas.[3]

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[2] Letter from Dr. Philip A. Butler, Chief, Gulf Coast Oyster Investigations, who kindly furnished the culch material for examination. "The results are interesting to me and enabled me to resolve some of the disparity in our setting data. We had exposed similar plates during the two previous years and on each occasion the heaviest concentration of setting was at the mid-water depth with the intensity of setting tapering off below and above this level. As you know, in 1952 the preponderance was nearest the bottom, and these results semed to conflict with the previous summers' results. Your analysis showing that the set at the lower levels was predominantly *Ostrea* corroborates our observations that in the previous summers adult *Ostrea* was virtually absent from this area."

The culch experiments show that there is a definite stratification of each species at both Port Aransas and Pensacola. The genus *Ostrea*, represented by *O. equestris* at Port Aransas and by this species and *O. frons* at Pensacola, attached near the bottom, whereas most of the spat of *C. virginica* were nearer the surface at both places. Random plankton tows supported these observations concerning the stratification of species. The tows were neither systematic nor quantitative, but mature *O. equestris* larvae were never found in the surface tows, while few *C. virginica* larvae were found in the bottom tows. The few *C. virginica* larvae in the bottom tows could have been captured as the weighted plankton net was lowered to the bottom. The attachment of *O. equestris* and *C. virginica* to slides (for physiological studies) also confirmed the differential stratification of the two species. These slides were often left in the water less than one week, and hence data from them were not affected as much by differential mortality which might obscure the actual pattern of attachment.

TABLE X

Average Numbers and Percentages of *O. equestris* and *C. virginica* That Attached at All Levels in Series B During Eleven Periods, June 6, 1951 to November 8, 1952.

Periods	Numbers		Percentages	
	O. equestris	*C. virginica*	*O. equestris*	*C. virginica*
6/6/51–8/5/51	30.1	10.9	73.4	26.6
7/25/51–10/21/51	57.2	8.4	87.2	12.8
9/1/51–12/30/51	52.6	7.8	87.1	12.9
10/21/51–3/22/52	1.0	0.3	75.0	25.0
12/30/51–5/11/52	0.0	0.0	......	......
3/22/52–6/2/52	34.0	20.3	62.7	37.3
5/11/52–6/28/52	55.9	26.2	68.0	32.0
6/2/52–7/27/52	16.3	15.3	51.5	48.5
6/28/52–8/28/52	27.1	6.0	82.0	18.0
7/27/52–10/19/52	20.4	2.8	87.9	12.1
8/28/52–11/8/52	48.6	10.3	82.5	17.5
Average	35.4	11.4	75.6	24.4

TABLE XI

Average Numbers of *O. equestris* and *C. virginica* Per Shell Per Day That Attached at All Levels in Series B During Eleven Periods, June 6, 1951 to November 8, 1952.

Period	*O. equestris*	*C. virginica*	Both species
6/6/51–8/5/51	5.00	1.80	6.80
7/25/51–10/21/51	0.66	0.10	0.76
9/1/51–12/30/51	0.44	0.06	0.50
10/21/51–3/22/52	0.01	0.01	0.01
12/30/51–5/11/52	0.00	0.00	0.00
3/22/52–6/2/52	0.80	0.49	1.29
5/11/52–6/28/52	1.16	0.55	1.71
6/2/52–7/27/52	0.30	0.28	0.58
6/28/52–8/28/52	0.44	0.10	0.54
7/27/52–10/19/52	0.24	0.03	0.27
8/28/52–11/8/52	0.68	0.14	0.82

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[3] Fouling of culch in the more northern waters of the East Coast of the United States is of economic importance. Manning (1952), Newcombe and Menzel (1945), and others have discussed the adverse effect of fouling on the strike of *C. virginica*, and stressed the need for clean culch. However, Zobell (1938), Cole and Knight Jones (1949), and Chesnut and Fahy (1953) found indications that slight fouling may enhance the strike.

There have been many observations on the stratification of setting of the several species of both genera of oysters, and many of these conflict with each other. Two of the most comprehensive publications on the two genera are those of Korringa (1941) who worked with *O. edulis* but reviewed the findings of previous workers on both genera, and Carriker (1951a) who dealt mainly with *C. virginica.*

Korringa (1941) obtained the greatest numbers of *O. edulis* spat near the bottom when stratified culch was put out at intervals of 25 cm., from 25 cm, above the bottom to the surface, even though his plankton tows had shown that there was no stratification of the mature larvae. He ascribed the heavier set on the bottom culch to the fact that there was less current velocity at the bottom than at the surface, and cites Prytherch (1929, 1934), who had found that *C. virginica* is likely to have the heaviest spatfall at those levels where larvae abound at the moment that currents are negligible. Cole and Knight Jones (1939) found a slightly better set near the surface in tanks, but later (1949) found similar results to those of Korringa in natural conditions. Gaarder and Spärck (1932) found that *O. edulis* has the heaviest spatfall on the bottom in Norwegian "polls," which have a salinity stratification with the most saline water at the bottom.

Quayle (1941) reports that *O. lurida* lives on the surface of mud flats or gravel bars located near the mouths of small rivers or streams in British Columbia. Elsey (1934) found that this species sets between the one and four foot tide marks in British Columbia. Hopkins (1936b, 1937) performed extensive experiments on *O. lurida* in the lower end of Puget Sound. He found that a few natural beds occur in sloughs or channels where they are never exposed. This species is grown commercially in "dikes" in the intertidal zone. Hopkins (1937) found that the best attachment occurred in these dikes when the culch on the bottom was covered by from three to ten feet of water, although there was some attachment when the culch was barely covered. Floating culch obtained the best strike at depths of 14 to 19 inches below the surface. Hopkins states that *O. lurida* is found in Yaquina Bay, Oregon, almost exclusively in deep water. He was unable to explain why this species should have attached much better at higher levels in the locality of his experiments.

Seki and Tanaka (1931, cited by Korringa, 1941) found that *O. denselamellosa* Lischke attached in greatest numbers 0.6 meter from the bottom. Ranson (1943) described the species of the genus *Ostrea* as prospering more offshore, but they do extend up estuaries where the salinity is high. They do not resist silting as does *Crassostrea,* and cannot live in the intertidal zone. They are found on the limits of the very lowest tides on bottoms rarely uncovered and down to depths of 20 to 85 meters. Castillo and Vergara (1907) say that *O. chiloensis* Phillippi occurs in natural beds in water four to five meters deep and cannot tolerate brackish waters.

More studies have been seen on the stratification of *Crassostrea,* especially *C. virginica,* than on stratification in the genus *Ostrea.* Churchill (1920) described the level of occurrence of *C. virginica* along the East Coast of the United States from near high water (South Carolina) to a depth of 130 feet (Patuxent River, Maryland). Prytherch (1929), Loosanoff (1933), A. W. H. Needler (1933), and Mackin (1946) found that in waters of high salinity the heaviest strike occurred in the intertidal zone. Loosanoff (1933) found that *C. virginica* strikes on the bottom in water of low salinity.[4]

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[4] Dr. R. W. Hiatt, University of Hawaii, in personal communication reported that *C. virginica,* introduced into Pearl Harbor, grows below low tide level. The salinity ranges between 10 and 20‰.

There have been many studies of the distribution of the larvae of *C. virginica.* J. Nelson and T. C. Nelson in their investigation over a period of years (J. Nelson 1901, 1908, and 1914; T. C. Nelson 1921a, 1922, 1924, 1925a, 1926, 1927, 1928, 1930, and 1952), T. C. Nelson and Perkins (1931) and Carriker (1951a) have shown that the larvae of this species are distributed throughout the water, sometimes stratified, sometimes not. The stratification, when it occurs, has been described as being influenced by current velocity, light, tidal stage and salinity. Some of the reports are conflicting.

Loosanoff and Engle (1940) found that the heaviest set of *C. virginica* in Milford Harbor, Connecticut, was near the bottom, where the salinity varied from 1‰ to 25–26‰ (the latter was more usual). Chestnut and Fahy (1952, 1953) performed experiments on the attachment of oysters in North Carolina at various levels in water of high salinity. They found abundant strike near the bottom, and attributed the intertidal occurrence of *C. virginica* in this region to failure of the spat near the bottom to survive. McDougall (1943) had obtained similar results at Beaufort, North Carolina.[5] But both *C. virginica* and *O. equestris* occur in this region, and the species were not distinguished.

Personal observations on the vertical distribution of *C. virginica* were made during the years from 1940 to 1946 in Virginia. In the James River on the "seed" grounds the majority of the strike was on the bottom below mean low water level. The salinity of the area in question was usually not over 15‰. On the other hand, observations near the mouth of the York River, where the salinity was about 20‰, showed that the spat on experimental and natural culch exhibited no special stratification but were more or less uniformly distributed from a depth of several meters to above low water mark. Observations on the seaside of the Eastern Shore of Virginia, where the salinity approaches that of the ocean, showed the majority of the spat to occur from low water mark to several feet above.

There have been some publications on several of the other species of *Crassostrea* also. Ranson (1943) says that *C. angulata* lives in the mouths of rivers that may be entirely fresh at ebb tide. The oysters occur in the brackish waters and form extensive beds where there is a constant flow of fresh water. There are a few on the intertidal rocks along the coast. (The distribution of *C. angulata* as described by Ranson is very similar to that of *C. virginica* in relation to salinity.) Chapman and Esveldt (1942) found no stratification of *C. gigas* in southern Willapa Bay, Washington, where the salinity ranges from 15 to 26‰. They stated, however, that in Puget Sound (higher salinity, see Hopkins, 1937) this species has a narrow zone of setting, from one to three feet, and "almost always well above the mean low tide." Wakiya (1929) says that *C. ariskensis* Fujita in Japan grows in low salinities. Mattox (1949) reports that *C. rhizophorae* (Guilding) occurs in the 1–2 foot intertidal level where the salinity ranges from 33–44‰.

According to Nelson (1938), the genus *Ostrea* occurs in the less turbid, more saline areas, whereas *Crassostrea* has been able to adapt itself to the more turbid, less saline areas such as river mouths and bays. Thomson (1954) says that species of *Crassostrea* are usually from intertidal reefs in areas of high salinities whereas they are subtidal in lower salinities. *Ostrea*, on the other hand, always occurs subtidally but only in areas of high salinity.

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[5] Letter from Mr. M. D. Burkenroad, Bogue Sound, North Carolina, September 6, 1951. ". . . . am sending a batch of oysters—on shells of live scallops from just below low tide in front of my house." (All specimens were *O. equestris.*) ". . . . in addition a sample of *O. equestris* from *Limulus* and some from *C. virginica,* which I had planted below low tide are included. The existence of the latter leads me to believe, in light of your work, that the common occurrence of *O. equestris* on scallops and horseshoe crabs is because there is little else to attach to below low tide here. But the question then arises, why can't *C. virginica* compete in deeper water here? Ordinary predators can't get at oysters on active substrata like scallops and crabs."

If only *C. virginica* is considered, the data suggest that it is actually unable to attach effectively in deep water of high salinity (Menzel, 1953). This is not an all or none phenomenon; even at Port Aransas, where the salinity was around 35‰, a few spat were found on the bottom, although none of these survived long in the culch experiments. At Pensacola the experimental culch did catch *C. virginica* nearer the bottom, but there the salinity was much lower during the period of the experiment (19.5 to 26.0‰).

Nelson and Perkins (1931) say that the larvae of *C. virginica* are distributed vertically by: (a) activity in response to salinity changes, (b) action of currents which sweep them into levels of increased current velocity, and (c) combinations of the above. If a salinity stratification is formed, the larvae react by swimming above the more saline waters into the lower levels of the overlying fresh waters, provided current velocities are low. If no halicline is present, there is no stratification of the larvae, or else there is a gradual decrease from bottom to surface without any sharp break; the larvae are most numerous at the level of the greatest current velocity. When the current is negligible the larvae are found in greatest numbers on the bottom. The larval counts are correlated with the strike. Korringa (1941) ascribes the heavier set (of *O. edulis*) on the bottom in depths of three or four meters to the fact that the current velocity is much less on the bottom. Prytherch (1929, 1934) had found previously that a heavy strike is likely to occur at those levels where larvae abound at the moment that currents are negligible.

These two hypotheses, Nelson's halicline and Korringa's current velocity theory, are not adequate to explain the stratification of setting at Port Aransas. Table I gives the surface salinities, and the few bottom salinities that were taken concurrently showed no haliclines. This would be expected in such shallow water, where the current was very strong. Current velocity readings made by members of the staff of the Institute of Marine Science at Port Aransas showed velocities up to almost two knots at the surface at strong ebb tide. Concurrent readings at the bottom showed the velocity to be about half that at the surface, and when the current velocity was less than about 0.75 knots at the surface none could be detected at the bottom. However, if salinity or current alone were the explanation of the stratification, then both species should react alike. It seems from the data presented above that larvae of *C. virginica* (and probably of other species of *Crassostrea*) are affected by salinity in such a way that the higher the salinity, the closer to the surface the larvae will set.

Ostrea, which does not occur in waters of low salinity, sets below the mean low water level in salinities which are high enough to confine *Crassostrea* to the intertidal zone. Sometimes the attachment is in the intertidal zone, but when this occurs there is a large tidal range. This is true for *O. edulis* (Ranson, 1943) and *O. lurida* (Hopkins, 1936b, 1937), but in each case there is a tidal range of from 15 to 20 feet. Perhaps factors such as low temperatures may explain the better set of these species in the intertidal zone (when covered by some depth of water) than in the deeper subtidal areas.

TABLE XII

Numbers of *O. equestris. O. frons* and *C. virginica* That Attached at Each Level in Two Plantings of Asbestos Plates at Pensacola, Florida.

Depth from Bottom	*O. equestris*			*O. frons*			*C. virginica*		
	A*	B†	Total	A	B	Total	A	B	Total
8 ft.	0	0	0	0	0	0	17	4	21
7 ft.	0	0	0	0	0	0	31	22	53
6 ft.	3	..	9‡	1	..	3‡	27	..	81
5 ft.	5	24	29	4	5	9	14	76	90
4 ft.	29	65	94	9	12	21	9	56	65
3 ft.	56	96	152	9	10	19	11	40	51
2 ft.	170	169	239	10	27	37	6	5	11
1 ft.	294	374	668	40	68	108	15	3	18
Totals		1191			197			390	

* A—Period from May 27 to June 6, 1952. 50 sq. cm. examined.
† B—Period from June 6 to June 16, 1952. 100 sq. cm. examined.
‡ —Plate in Series B lost. Total number calculated.

TABLE XIII

Number of Spat of Each Species on Each of Ten Twenty-Five Square Centimeter Areas on Bottom Surface of Plate

This asbestos plate was suspended 3 feet above bottom at Pensacola, Florida, from May 27 to June 6, 1952.

Block Number	*O. equestris*	*O. frons*	*C. virginica*	Total
1	29	4	3	36
2	27	4	2	33
3	28	3	5	36
4	29	5	4	36
5	33	5	4	42
6	27	3	3	33
7	27	5	8	40
8	29	4	5	38
9	27	4	6	37
10	31	7	3	41
Total	287	44	41	372
Mean	28.7	4.4	4.1	37.2

Chi Square (*O. equestris*) = 1.26
Chi Square (*O. frons*) = 2.82
Chi Square (*C. virginica*) = 3.56
Chi Square (Total) = 1.85

TABLE XIV

Percentage of *O. equestris, O. frons* and *C. virginica* That Attached at Each Level at Pensaloca, Florida: Both Series Pooled.

Level from Bottom	*O. equestris*	*O. frons*	*C. virginica*
2.43 M.	0.0	0.0	5.4
2.13 M.	0.0	0.0	13.6
1.82 M.	0.8	1.5	20.7
1.52 M.	2.4	4.6	23.1
1.21 M.	7.9	10.7	16.7
0.91 M.	12.8	9.6	13.0
0.61 M.	20.1	18.8	3.0
0.30 M.	56.1	54.8	4.6

PERCENTAGE OF TOTAL OF EACH SPECIES:

O. equestris —67.0
O. frons —11.1
C. virginica —21.9

GROWTH STUDIES

Introduction

O. equestris was originally described by Thomas Say (Binney, 1858) as a "small" oyster. No specimen over 35 mm. long was ever collected in the vicinity of the Laboratory at Port Aransas. However, specimens dredged off Padre Island in the Gulf of Mexico measured up to 50 mm. in length. These oysters had relatively thin shells and appeared to be actively growing, unlike the larger specimens in Aransas Pass, which had thickened shells and appeared to have stopped any appreciable increase in shell length. Specimens attached to scallop shells (*Pecten* sp.) received from North Carolina were also larger than those in the Pass. These measured up to 40 mm. in shell length. Gunter (1951b) found specimens of this species over 70 mm. long off the Texas Coast.

Studies were made to compare the growth of *O. equestris* with that of *C. virginica.* Gunter (1951a,b) is the only author that has been found to give any information on the growth of *O. equestris*. He collected this species from an oil well platform off the Texas Coast (as well as in Louisiana) and found that some individuals had reached a length of 72 mm. within a year. There have been many investigations of the growth of *C. virginica* along the Atlantic and Gulf Coasts of the United States. Some of these are as follows: Stafford (1913) in Canada; Churchill (1921), Loosanoff (1947), Loosanoff and Nomejko (1949) in the Long Island-Connecticut region; Nelson (1922) in New Jersey; and Ryder (1885) and Beaven (1949, 1952) in the Chesapeake Bay area. Dean (1892), Moore (1905), and Glaser (1905) have reported on this species from North Carolina and South Carolina. Brice (1896), Ingle (1950), Ingle and Dawson (1952), and Butler (1952a,b, 1953a) have published on its growth in Florida. Several investigators have reported on its growth in Louisiana waters, including Moore (1899), Moore and Pope (1910), Menzel (1951), and Hopkins, Mackin and Menzel (1953). Two publications have been found from Texas (Gunter, 1951b, and Baughman and Baker, 1951).

Results of the Experiments

The results of the observations of growth are given in Tables XV to XXVI, which present data on the shell increments and calculations made from these increments. The first three experiments listed in the tables are comparisons of the two species, whereas Experiments IV and V concern only *O. equestris.* The results of the first three studies will be discussed first.

Experiments show that the shells of *C. virginica* grow faster than those of *O. equestris* as was expected from general observations. Since these experiments were not designed primarily as growth experiments, no detailed analysis will be made. However, the data do show some interesting facts.

It is seen from Tables XVI, XVIII and XX that the average gain per day in Index I for *C. virginica* was best after the initial period (*i.e.*, in the second period in Experiment I and III, and in the fourth period in Experiment II). But the average gain in Index I per day for *O. equestris* was always best during the first interval after planting. There was a progressive decrease during the remainder of the periods (except in Experiment I, where there was little shell growth during the second interval).

The slope of the regression line of time to Index I of *C. virginica* was six times greater than that of *O. equestris* in Experiment I, and five times greater in Experiment II. The data show that the percentage of increase in length of *C. virginica* was from two to three times that of *O. equestris*, but the percentage increase in height was usually less than twice as great (Tables XVI, XVIII and XX).

Of the three experiments, Experiment II was the only one in which oysters were suspended at different depths to measure the effects of depth on growth. The experimental *C. virginica* at 0.5 meter from the surface were in the water for a period of only

TABLE XV

Experiment I

Shell Measurements of Ten *O. equestris* and Six *C. virginica* at Intervals From August 6, 1951 to May 11, 1952

Date	Average size, mm. Length	Average size, mm. Height	Index I, sq. mm.
Aug. 6, 1951			
O. equestris	13.1	10.1	132
C. virginica	18.5	15.4	285
Sept. 6, 1951			
O. equestris	20.5	18.9	387
C. virginica	30.3	25.3	767
Oct. 21, 1951			
O. equestris	21.9	19.0	416
C. virginica	44.0	36.7	1,615
Dec. 30, 1951			
O. equestris	25.3	22.8	577
C. virginica	52.9	43.1	2,280
March 22, 1952			
O. equestris	29.0	24.2	702
C. virginica	61.6	51.8	3,191
May 11, 1952			
O. equestris	29.0	25.0	725
C. virginica	65.2	53.3	2,475

TABLE XVI

Experiment I

Comparative Growth of *O. equestris* and *C. virginica* During Each of Six Periods

Period	Gain in Index I Per Day	Percentage Increase Length	Percentage Increase Height	Percentage Increase Index I
8/6/51–9/6/51				
O. equestris	8.2	56	87	193
C. virginica	15.5	64	64	169
9/6/51–10/21/51				
O. equestris	0.7	7	1–	7
C. virginica	18.8	45	45	110
10/21/51–12/30/51				
O. equestris	2.3	20	20	38
C. virginica	9.2	20	17	41
12/30/51–3/22/52				
O. equestris	1.5	14	6	21
C. virginica	11.0	15	20	40
3/22/52–5/11/52				
O. equestris	0.5	1–	3	3
C. virginica	5.7	6	3	9
8/6/51–5/11/52				
O. equestris	2.1	121	147	449
C. virginica	11.4	252	246	1119

TABLE XVII

Experiment II

Shell Measurements of *O. equestris* and *C. virginica* 0.5 Meter and 3.5 Meters Above Bottom, at Intervals From August 6, 1951 to May 11, 1952.

	Average size, mm.					
	Length		Height		Index I, sq. mm.	
Date	0.5	3.5	0.5	3.5	0.5	3.5
Aug. 6, 1951						
O. equestris	8.8	8.5	7.9	7.9	70	67
C. virginica	10.0	9.5	8.7	8.6	87	82
Sept. 6, 1951						
O. equestris	17.2	17.6	15.8	15.9	272	280
C. virginica	23.3	21.6	18.6	15.1	433	326
Oct. 21, 1951						
O. equestris	23.0	20.9	19.2	18.3	442	382
C. virginica	32.7	*	28.2	*	922	*
Dec. 30, 1951						
O. equestris	25.3	*	22.1	*	599	*
C. virginica	49.1	......	35.2	......	1728	......
March 22, 1952						
O. equestris	29.5	......	24.0	......	708	......
C. virginica	67.5	......	43.2	......	2916	......
May 11, 1952						
O. equestris	29.6	......	25.8	......	764	......
C. virginica	73.2	......	44.5	......	3257	......

* Lost.

TABLE XVIII

Experiment II

Comparative Growth of *O. equestris* and *C. virginica* Planted 0.5 Meter and 3.5 Meters Above Bottom, During Each of Six Periods.

	Gain in Index I Per Day		Percentage Increase					
			Length		Height		Index I	
Date	0.5	3.5	0.5	3.5	0.5	3.5	0.5	3.5
8/6/51–9/6/51								
O. equestris	6.5	7.0	95	107	100	101	288	318
C. virginica	11.2	7.9	133	127	114	75	398	297
9/6/51–10/21/51								
O. equestris	3.8	2.3	33	19	21	15	62	36
C. virginica	10.8	*	40	*	51	*	113	*
10/21/51–12/3/51								
O. equestris	1.7	4.1	10	146	15	131	26	470
C. virginica	11.5	....	50	......	25	......	87	......
12/30/51–3/22/52								
O. equestris	1.8	*	16	*	8	*	26	*
C. virginica	14.3	....	37	......	23	......	68	......
3/22/52–5/11/52								
O. equestris	1.1	....	1	......	7	......	8	......
C. virginica	6.8	....	8	......	3	......	11	......
8/6/51–5/11/52								
O. equestris	2.1	....	236	......	226	......	991	......
C. virginica	11.4	....	632	......	411	......	3643	......

* Lost.

31 days and the experimental *O. equestris* for 76 days, so they can be compared for only the first 31-day period. It is seen from Table XVIII that the Index I increase per day was better at the bottom for *C. virginica* and was almost as good for *O. equestris.* During the second period, growth of *O. equestris* was much better at the level 0.5 meter from the bottom than at the level 3.5 meters above the bottom. The comparative figures for percentage of increase bear out the above statements.

The regression coefficients for the two species at the two depths are found in Table XXVI. During the first period the regression coefficient for *C. virginica* was only slightly greater at a depth of 0.5 meter from the bottom than at 3.5 meters above the bottom. During this period, *O. equestris* had a slightly lower regression coefficient at the bottom level than at the top level. However, for the entire period from August 6 to October 21, 1951, the regression coefficient of *O. equestris* was larger at the lower level

TABLE XIX

Experiment III

Shell Measurements of Twelve *O. equestris* and Five *C. virginica* at Intervals From June 28, 1952 to November 11, 1952.

Date	Average size, mm. Length	Height	Index I, sq. mm.
June 28, 1952			
O. equestris	16.0	13.1	210
C. virginica	20.5	15.5	317
July 27, 1952			
O. equestris	20.2	18.7	378
C. virginica	27.0	22.5	607
Aug. 27, 1952			
O. equestris	22.0	19.0	418
C. virginica	39.0	28.5	1112
Oct. 18, 1952			
O. equestris	23.0	19.1	439
C. virginica	45.0	31.0	1395
Nov. 8, 1952			
O. equestris	22.9	19.5	447
C. virginica	46.5	32.5	1512

TABLE XX

Experiment III

Comparative Growth of *O. equestris* and *C. virginica* During Each of Five Periods

Period	Gain in Index I Per Day	Percentage Increase Length	Height	Index I
6/28/52–7/27/52				
O. equestris	5.8	26	42	80
C. virginica	9.8	33	42	89
7/27/52–8/27/52				
O. equestris	1.3	6	1	10
C. virginica	16.3	44	27	83
8/27/52–10/18/52				
O. equestris	0.4	4	1	5
C. virginica	5.6	16	9	26
10/18/52–11/8/52				
O. equestris	0.4	–1	2	2
C. virginica	5.0	3	4	7
6/28/52–11/8/52				
O. equestris	1.8	43	49	113
C. virginica	8.8	130	104	370

than at the upper. From these calculations it may be said that these oysters grew slightly better at 0.5 meter than at 3.5 meters above the bottom in water 4 meters deep.

Experiments IV and V were really only one experiment using two different initial size groups (from culch planted July 14, 1951), but they have been tabulated separately for convenience. These experiments contained only *O. equestris* and lasted for only 31 days. They are described here because as far as is known they are the only growth experiments in which three shell measurements have been made on such small oysters.

The data are given in Tables XXI to XXVI. The results are treated similarly to those of the first three experiments except that Index II (product of length, height and thickness) was also calculated, and individual growth measurements are given for each oyster as well as the average for all oysters.

TABLE XXI

Experiment IV

Individual Shell Measurements in Millimeters of Seventeen *O. equestris* 0.5 Meter Above Bottom on August 8, 1951, and on September 7, 1951.

	August 8, 1951			September 7, 1951		
	Length	Height	Thickness	Length	Height	Thickness
	2.4	2.0	0.3	16.0	16.0	2.3
	3.0	3.0	0.4	11.5	7.5	1.5
	1.2	1.2	0.5	9.5	10.0	1.2
	4.8	4.6	0.6	15.0	14.5	2.0
	4.3	4.0	0.5	11.0	10.0	1.3
	4.4	4.3	0.4	9.5	9.0	1.4
	4.3	4.4	0.4	10.5	9.0	1.1
	4.3	4.5	0.6	16.5	11.0	2.7
	2.9	2.7	0.3	16.0	14.0	2.1
	2.7	2.3	0.3	13.5	9.0	2.0
	4.1	3.1	0.4	12.0	10.0	2.0
	4.3	4.6	0.5	11.0	12.0	1.3
	4.4	4.5	0.6	13.0	13.0	2.0
	3.6	2.8	0.4	18.5	18.0	2.1
	5.1	5.0	0.6	14.0	12.5	2.2
	5.2	5.0	0.7	11.0	11.0	1.7
	4.1	3.6	0.5	13.0	11.0	2.6
Av.	3.8	3.6	0.5	13.1	11.6	1.9
	Index I	13.7			152	
	Index II	6.8			289	

TABLE XXII

Experiment IV

Individual Shell Measurements in Millimeters of Five *O. equestris* 1.5 Meters Above Bottom on August 8, 1951 and on September 7, 1951.

	August 8, 1951			September 7, 1951		
	Length	Height	Thickness	Length	Height	Thickness
	3.3	3.5	0.5	18.0	14.0	2.6
	3.1	3.3	0.5	11.0	13.0	2.8
	4.0	3.7	0.6	21.0	16.0	2.7
	3.0	3.0	0.4	17.0	16.5	2.5
	4.0	3.5	0.6	16.0	16.0	2.5
Av.	3.5	3.4	0.6	16.6	15.1	2.6
	Index I	11.9			250.5	
	Index II	6.0			651.5	

In both experiments the regression coefficient for Index I (Table XXVI) was much greater at the upper level than at 0.5 meter from the bottom. However, at each depth, this figure was nearly the same in the two experiments. The oysters of the smaller initial size group in Experiment IV showed only a slightly better growth than those of the larger initial size group in Experiment V, on the basis of the regression coefficient for Index I. At the depth 0.5 meter from the bottom, the oysters in Experiment V showed a greater gain per day for Index I than did the smaller group in Experiment IV, and the gain per day for Index I at a depth of 1.5 meters from the bottom was about the same for the two experiments (Table XXV). But, if the gain per day for Index II is considered, where thickness is also taken into account, it is seen from Table XXV that

TABLE XXIII

Experiment V

Individual Shell Measurements in Millimeters of Two *O. equestris* Planted 0.5 Meter Above Bottom on August 8, 1951 and on September 7, 1951.

	August 8, 1951			September 7, 1951		
	Length	Height	Thickness	Length	Height	Thickness
	9.0	9.5	1.0	14.5	14.0	3.1
	8.0	8.0	0.8	15.0	14.0	2.0
Av.	8.5	8.8	0.9	14.8	14.0	2.6
Index I		74.8			250	
Index II		67.3			538	

TABLE XXIV

Experiment V

Individual Shell Measurements in Millimeters of Seven *O. equestris* 1.5 Meters Above Bottom on August 8, 1951 and on September 7, 1951.

	August 8, 1951			September 7, 1951		
	Length	Height	Thickness	Length	Height	Thickness
	7.0	8.5	1.2	19.0	16.5	3.6
	9.0	10.5	1.4	21.0	17.5	3.2
	7.0	7.0	1.0	16.0	10.0	3.0
	8.5	9.5	1.0	18.0	20.0	5.5
	9.0	8.0	1.0	23.0	18.0	3.0
	11.5	12.0	1.5	13.5	16.0	4.3
	13.5	11.0	1.6	21.5	17.0	4.0
Av.	9.0	9.5	1.2	18.9	16.4	3.8
Index I		86.5			310	
Index II		103.5			1178	

TABLE XXV

Comparative Growth of *O. equestris* in Experiments IV and V During Period From August 8, 1951 to September 7, 1951.

	Gain per Day		Percentage Increase		
Depth from Bottom	Index I	Index II	Length	Height	Thickness
0.5 Meter					
Exper. IV	4.6	9.4	244	222	280
Exper. V	5.8	16.7	74	59	189
1.5 Meters					
Exper. IV	8.0	21.5	375	344	420
Exper. V	7.8	39.1	107	72	216

the growth of the oysters of larger initial size in Experiment V was much greater than that of the smaller oysters in Experiment IV. This same table shows that the percentage of increase was much greater for the smaller size group. These figures also show that the thickness had the greatest increase and the length next greatest.

TABLE XXVI

Regression Formula (Estimated Y) of Index I for Growth Experiments I Through V

Exper.	Species	Period	Depth	"b"	Plus
I	*O. equestris*	8/6/51–5/11/52	0.5 M.	1.9X	247
I	*C. virginica*	8/6/51–5/11/52	0.5 M.	11.4X	476
II	*O. equestris*	8/6/51–5/11/52	0.5 M.	2.3X	175
II	*C. virginica*	8/6/51–5/11/52	0.5 M.	11.8X	48
II	*O. equestris*	8/6/51–10/21/52	0.5 M.	5.3X	76
II	*O. equestris*	8/6/51–9/6/51	0.5 M.	6.5X	60
II	*C. virginica*	8/6/51–9/6/51	0.5 M.	11.2X	75
II	*O. equestris*	8/6/51–10/21/51	3.5 M.	4.4X	89
II	*O. equestris*	8/6/51–9/6/51	3.5 M.	6.9X	59
II	*C. virginica*	8/6/51–9/6/51	3.5 M.	7.8X	74
III	*O. equestris*	6/28/52–11/8/52	0.5 M.	1.5X	276
III	*C. virginica*	6/28/52–11/8/52	0.5 M.	9.0X	372
IV	*O. equestris*	8/8/52–9/7/52	0.5 M.	4.6X	9
IV	*O. equestris*	8/8/52–9/7/52	1.5 M.	8.0X	3
V	*O. equestris*	8/8/52–9/7/52	0.5 M.	4.4X	71
V	*O. equestris*	8/8/52–9/7/52	1.5 M.	7.5X	78

Summary and Discussion

These studies indicate that *C. virginica* grows to a much larger size than does *O. equestris* during the same period of time. At approximately two months, six months, ten months, and eleven months after attachment, the two species had attained the following average measurements:

O. equestris

Two months—19 mm. in length; 16.5 mm. in height; 3.8 mm. in thickness.
Six months—23 mm. in length; 19.5 mm. in height.
Ten months—29.5 mm. in length; 26 mm. in height; 13.5 mm. in thickness.
Eleven months—29 mm. in length; 25 mm. in height; 13.5 mm. in thickness.

C. virginica

Six months—46.5 mm. in length; 32.5 mm. in height.
Ten months—75 mm. in length; 45 mm. in height; 23 mm. in thickness.
Eleven months—65 mm. in length; 55 mm. in height; 23 mm. in thickness.

Small *O. equestris*, under 5 mm. in diameter, did not increase in size more than did individuals between 5 and 10 mm. in diameter during a period of 31 days, if the product of all the linear measurements is taken as the index of size. *O. equestris* (growing on flat surfaces) reached in 31 days a length and height nearly two-thirds that of ten- and eleven-month-old specimens, but the thickness was less than one-third that of the older individuals.

No definite conclusions can be reached about the comparative rates of growth at levels of 0.5 meter from the bottom and near the surface. The experimental periods were not long enough and the results were not consistent.

There seems to be little difference between the two species in the rate of increase in length and height up to about 15 to 30 days of age, or until the shell has attained a length of about 10 mm. This statement is supported by the fact that the spat of the two species, on culch that had been planted for a month or less, were nearly the same size. In the first three growth experiments, the differences in linear measurements of the two species were less in proportion in the younger than in the older spat. Similar results were obtained from other examinations and measurements of spat of both species on culch. These supplementary data are not presented.

The shell measurements bear out the impression from the general observations that the young spat of both species are almost round, *i.e.*, the height is as great as the length. As they grow larger, however, the length increases more in proportion to the height, and this proportional increase in length is much greater in *C. virginica* than in *O. equestris*. Larger *O. equestris* sometimes are as high as long, whereas *C. virginica* are usually longer than high. Of course, there are individual exceptions, which have been observed more often in *C. virginica*. It is more common for *C. virginica* to be rounded than for *O. equestris* to be elongated. Preliminary data indicate that *O. equestris* at Port Aransas reaches the maximum length and height rather rapidly, and thereafter most of the increase is in thickness of the shell. The individual measurements given for *O. equestris* in Experiments IV and V illustrate the individual variation in growth found in both species in all of the experiments.

DISEASES, PREDATORS AND MORTALITY

Introduction

No special experiments were performed to determine for the two species of oysters the mortality caused by disease and predators. However, all dead oysters in the culch and growth experiments were examined, and the cause of death was noted if it could be determined. Oysters from Port Aransas have been checked by Dr. J. C. Mackin for the fungus parasite *Dermocystidium marinum* Mackin, Owen and Collier. The writer examined many oysters for the protozoan parasite *Nematopsis ostrearum* Prytherch. Notes were made on other known enemies.

Mortality was recorded in ten growth experiments, and in the culch examinations. However, none of the detailed data are presented here because they are fragmentary and the results inconclusive. A few generalizations are given on the mortality of oysters at Port Aransas. These are based on data from the various culch and growth experiments and on field observations.

Diseases and Predators

Nematopsis spp. were seen in both species of oysters. However, even though Prytherch (1938, 1940) thought that this protozoan was a serious parasite, later investigators have found no correlation between the occurrence of this gregarine and mortality in oysters (Galtsoff, Engle and Calderwood, 1947; Sprague, 1949; Landau and Galtsoff, 1951; Owen, Walters and Bregan, 1951; Sprague and Orr, 1952.)

Dr. J. C. Mackin (personal communication), using the Ray technique (Ray, 1952a, b), found no *Dermocystidium marinum* in a sample of *C. virginica* about one year old that were used in one of the unreported growth experiments. In this particular experiment, during the summer months there was no mortality that was not caused by known predators. It has been found (Mackin, Owen and Collier, 1950; Mackin, 1951; Ray, Mackin and Boswell, 1953; Andrews, 1953; Ray, 1953) that *D. marinum* is a serious pathogen and causes extensive mortality, especially during the warmer months, in areas where it is endemic.

Cliona celata Grant, one of the boring sponges, was sometimes abundant in the shells of oysters of both species in the study area. Several investigators have stated that boring sponges could be a serious enemy of oysters (Topsent, 1887, 1900; Cary, 1907; de Laubenfels, 1947; Old, 1941 and 1942), but no mortality from this cause was observed during the present investigation.

A polyclad flatworm, *Stylochus* sp. (probably *S. ellipticus* Girard) was found during the investigation to have killed spat of both species of oysters. However, they were never found in large numbers. *S. frontalis* Verrill has been reported to cause severe mortality and financial loss in Florida (Churchill, 1921; Danglade, 1919; Pearse and Wharton, 1938).

The mudworm, *Polydora websteri* Hartman, was seen only in *C. virginica* and never in large numbers. Several investigators have indicated that mudworms may cause extensive damage (Nelson and Stauber, 1940; Lunz, 1941; Mackin and Cauthron, 1952).

The stone crab, *Menippe mercenaria* (Say), which is very common in the vicinity of Port Aransas, kills many oysters. Cary (1907) reported the damage done by these crabs in Louisiana, and later Baughman and Baker (1951) indicated that this crab may be a serious enemy of oysters in Texas waters. On several occasions these crabs killed more than 50% of the spat on culch near the bottom in the experiments on stratification of strike. From field observations, it was estimated that the percentage of oysters killed by stone crabs was 5–25%.

Lunz (1947) and Carriker (1951b) have shown that the blue crab, *Callinectes sapidus* Rathbun, is an enemy of *C. virginica,* and especially of small individuals. These crabs are often abundant at Port Aransas, but no observations were made on predation by them.

Stauber (1945) reported that oyster crabs, *Pinnotheres ostreum* (Say), killed many oysters in New Jersey. Sandoz and Hopkins (1947) did not find that they killed oysters in Virginia, but did find that the oysters that contained these crabs were in poorer condition than those that did not. *Pinnotheres* sp. (probably *P. ostreum*) was found on only three occasions, and only in *C. virginica,* at Port Aransas. Hedgpeth (1953) reported *P. ostreum* from the Rockport, Texas, area.

The oyster conch, *Thais haemostoma,* was numerous in this locality and caused severe oyster mortality. Several investigators have described the damage done by oyster conchs in the Gulf of Mexico region (Moore, 1898; Cary, 1907; Burkenroad, 1931b; Baughman and Baker, 1951; Butler, 1953b,c). No experiments were performed at Port Aransas to determine the rate of destruction of oysters by these snails, or whether they showed any preference between the two species. But from observations of the other experiments and surveys in the field, the conchs seemed to exercise no choice in the species of oysters, but were destructive to both species. Observations in the field revealed that the majority of the dead oysters (or at least the majority of those with right valves still intact) had been killed by conchs (78% in June, 1951, and 95% in June, 1952).

Although it was found in considerable numbers in the less saline waters inland from Aransas Pass, the boring clam, *Martesia smithii* (Tryon), was not common in the immediate vicinity of the laboratory at Port Aransas. The clams were seen only in the shell of *C. virginica.* Several investigators have discussed the effect of boring clams on oysters (Moore, 1899; Cary, 1907; Galtsoff, Prytherch, Smith and Koehring, 1935; Federighi and Collier, 1935; Pearse and Wharton, 1935).

The sheepshead fish, *Archosargus probatocephalus,* is probably an enemy of considerable importance. Mr. Will Kucera, a student at the Institute of Marine Science during the summer of 1951, made a study of the stomach contents of several species of fishes in this locality. He found the stomach of some sheepshead full of oyster shells. Almost all the shells were of *O. equestris.* The absence of *C. virginica* shells in the stomach contents was undoubtedly due to the fact that *C. virginica,* in this locality of high salinity, occurs mainly in the intertidal zone, and sheepshead usually feed some distance below the surface.

Discussion

There is probably a higher rate of mortality in newly attached spat than in any other phase of the oyster's life after it becomes sessile. The case mentioned above (p. 91), in which over 2000 *C. virginica* attached to a surface area of less than 60 square centimeters, illustrates one reason why there is such high mortality. As Coe (1932c) pointed out, more individuals of sessile species attach themselves in a few days than find space for continued growth. Thus oysters attach so abundantly that they compete for Lebensraum, not only with themselves but also with other sessile organisms. Korringa (1941) estimated that 9 out of 10 larvae of *O. edulis* perish between the time of setting and the following winter, and Loosanoff and Engle (1940) have estimated that there is sometimes from 86% to 100% mortality in spat of *C. virginica* before they reach 2 months of age. Andrews (1948) found a mortality rate as high as 98% in this species from time of attachment in June to the following November.

Some information on the heavy mortality of young oysters was gained from an analysis of the culch data. The average number per shell of both *O. equestris* and *C. virginica* was 34.8 in Series A, in which the shells were usually in the water about one month during the season of attachment. The average number was 46.8 per shell for Series B, in which the shells were in the water twice as long. The culch in Series B would not be expected to have twice as many spat, because sessile organisms including oysters had preempted space for attachment and otherwise rendered the culch less suitable for attachment of oysters. Measurements of the spat in both series, however, indicated that about 75% had been attached less than one month. The data on the mortality is misleading because many of the oysters died and left no trace of ever having attached. This was true especially in Series A, where there was a proportionally larger number of small oysters. Even in Series B the numbers of dead counted were minimum numbers, because only dead oysters and attached left valves were counted. The average mortality for both species was about 6% in Series B and less than 2% in Series A. Both figures are far too low for the actual mortality.

The growth experiments gave some additional information on the mortality of small oysters. It was found that the very young oysters, like those in growth Experiments IV and V, had a much higher mortality than older oysters. In these Experiments (IV and V), approximately one-third of the oysters died within one month, and no evidence could be seen of any predation or known cause of death. The slides to which these experimental oysters had attached had become fouled again with sessile organisms when examined after a period of 30 days. All such foulants had been removed, however, when the oysters were measured one month previously. Thus competition, to which has been ascribed some of the death of newly attached spat, had been removed for a while at least.

The greater part of the mortality in the other growth experiments, in which small oysters of between one and two months of age were used, occurred within two months after the experiments were started. After the first two months, no oysters died, other than those killed by conchs in some experiments. In only one instance did an oyster die that was six months of age, in which the death was not accountable to predation by conchs. One experiment, using *C. virginica* between 60 and 70 mm. in length that were about one year old, had no mortality during the summer of 1952 that was not caused by oyster conchs.

Conclusions

A few general conclusions can be drawn from the mortality studies on the two species. Mortality was very high during the first month or so after attachment, and then became much less. The majority of the deaths of the larger oysters in both species could be attributed to predators, the oyster conch being the most serious. Stone crabs and sheepshead fish also undoubtedly destroyed considerable numbers of young oysters in unprotected places.

There is a prolific attachment of both species of oysters every year, but it is estimated that few oysters of either species live longer than about one year in the study locality (vicinity of Port Aransas). This high mortality is caused by the predators described above. It is noteworthy that large *C. virginica* had no mortality during the summer months, except that caused by the conch, whereas oysters of similar size under similar conditions in Louisiana (where *Dermocystidium marinum* occurs) would have had considerable mortality.

FEEDING OBSERVATIONS

Introduction

There have been many studies on the feeding behavior of oysters, especially of *C. virginica* and *O. edulis*. Yonge (1926) studied the feeding of *O. edulis* and traced the passage of food into the mouth and its subsequent digestion and elimination. Nelson (1921b, 1923a,b, 1927, 1933, and 1938) investigated various aspects of feeding and digestion in *C. virginica* and other species. There have been many other publications dealing with feeding in several species of oysters, and these are mentioned below as they pertain to the present research.

Lotsy (1893), Grave (1916), Morse (1944), Loosanoff (1949), and Pomeroy (1952) are among those who have stated that oysters exercise a selectivity in their feeding habits. But Kellogg (1915) and later Yonge (1926) said that the selection of food is by size alone. Yonge (1926) said that oysters feed with maximum efficiency only when the water is clear. But Nelson (1950) stated that oysters can feed in water so muddy "that a white saucer disappears 8 inches below the surface." Elsey (1935) found that oysters not only must effect the gross separation of food and dirt on the surface of the plicae (gills) but also must get rid of the finer particles which are passed through the ostia of the gills. Both Elsey and Nelson (1938) found that the *Crassostrea* type can withstand more turbid water than the *Ostrea* type. Nelson described a promyal chamber, which is more or less a direct passage to the exterior for silt-laden water. He ascribed the ability of the *Crassostrea* type to live in the more turbid estuarine areas to this anatomical feature.

Thus, there are two schools of thought on the selectivity of feeding in oysters. Each group has experimental evidence to support its claims. However, the group which holds that there is no selectivity of feeding except as regards size of particles, that only those particles are rejected that are too large to be taken into the digestive tract, worked on the genus *Ostrea.* The group which found selectivity in food particles regardless of size experimented mainly with *Crassostrea virginica.* There is additional evidence that *Crassostrea* not only selects its food, but also can effectively rid itself of the silt that is usually present in the estuarine areas where it occurs most abundantly.

The investigations at The Institute of Marine Science, Port Aransas, Texas, lent themselves admirably to a comparison of the feeding reactions of the two species under more or less natural conditions. The use of the small oysters attached to glass slides, on which they were observed under magnification, has been described above. The use of various suspensions lent itself to experimentation in comparing the feeding reactions of the two species, representing the two genera *Ostrea* and *Crassostrea.*

Description of Feeding in Oysters

Oysters are plankton feeders and strain out suspended matter from the water that is pumped by the ciliary action of the gills. According to MacGinitie (1941), a sheet of mucus covers the gills; it is this mucus which catches the food from the water passing through the gills. The food-laden strings of mucus are carried toward the palps surrounding the mouth. Nelson (1923a,b) says that the more bulky materials are consigned to the ventral grooves of the gills. In the passage to the palps they evoke a more conspicuous secretion of mucus than do particles at the base of the gills, so that the large particles become even larger and are less apt to be admitted between the palps. Thus the palps may cause the mass to be ejected as pseudofaeces. Allen (1914) found that there is a reflex erection of ridges in the palps in fresh water mussels that beat away from the mouth in case the food is rejected as pseudofaeces. Kellogg (1915) described a similar arrangement in other lamellibranchs. Grave (1916) states that there is a reversal of the beat in certain tracts of cilia in the palps, which aids in the sorting of food, but others have not confirmed this.

Yonge (1926) found that the beat of the cilia in the bottom of the grooves between the plicae of the gills is toward the base of the demibranchs, whereas the beat of the cilia on the filaments is toward the free margin of the gills, and that only small particles are carried to the base of the gills. He says that there are two selective mechanisms on the gills—one on the surface which causes the particles to drop to the mantle, and one on the free margin which carries the small particles to the palps and rejects the large particles to the mantle to be eliminated. In the same paper, he says that the contraction of the gills results in a transfer of the food to the mantle and thus offers a third selective mechanism.

Yonge (1926) described the action of the palps in detail. He found that particles from the free margin of the gills are transferred to the middle of the faces of the inner palps, whereas the smaller particles from the gills are passed into the grooves between the palps. Here, because of weaker ciliation in the grooves, particles are passed onto the lower folds between the inner palps; these lower folds lead to the mouth. Particles are carried back toward the apex of the palps to within a short distance of the tips. Here they meet a forwardly directed current from the tips which creates a vortex, and the particles are rolled into a mass. After attaining a certain size, these fall off to the mantle, either directly from the left palps or by way of them from the right palps. He describes five ciliated tracts on the folds of the inner palps which beat in different directions and carry food either toward the mouth to be swallowed or toward the apices to be rejected as pseudofaeces. The cilia on the folds and in the furrows between them act as an efficient sorting mechanism, with the small particles going toward the mouth and larger particles (and small particles embedded in copious mucus) going to the apex.

Yonge (1926) gives some information on the feeding of small oysters. He mentions a size of 1 mm., but does not say whether the data apply also to spat of larger sizes. He found that the ciliary mechanisms concerned with the elimination of surplus matter were well developed, and that the cilia were larger and more active in the spat than in the adult. The palps are relatively of immense size. There are no folds in the palps, but they do have grooves in which the cilia beat toward the distal end. He found only one ciliary tract leading to the base, but several tracts that led across the palps. In experiments in which particles were placed on the palps, only a minute portion succeeded in passing into the mouth; the majority were passed rapidly to the depression at the juncture of the outer palps, where they were rolled into a ball and finally fell to the mantle.

Nelson (1923a) describes the action of the cilia on the palps and gills of *C. virginica* in oysters under 3 mm. in length observed under the microscope. The separation of particles, *i.e.*, inorganic from organic, is accomplished partly by the gills but mainly by the palps. Particles on the gills are entangled in mucus in two paths: either ventrad to the groove formed by the ventral margin of the gill lamella, or dorsad to the dorsal groove along the bases of the gill filaments. The mucus-enclosed particles form into slime strings and are carried anteriad to the palps where they may pass between the faces of the palps into the mouth or they may be pushed off into the mantle, ventrad to the palps. At intervals, the material that has accumulated is expelled from the mantle cavity by quick contractions of the adductor muscle. A larger portion of the material from the dorsal groove of the gills is accepted than from the ventral groove. Large particles, such as sand grains, are assigned to the ventral groove and become more bulky because they are covered with a copious mucus and hence are more likely to be rejected. The smaller particles, which go to the dorsal margin, have less mucus, and on reaching the palps are passed through the opposing faces of the palps where further selection takes place. Small particles are picked out of the mucus mass and carried dorsad to the mouth.

Allen (1914, 1921), Kellogg (1915), and Churchill and Lewis (1924) are others who have reported on the action of the palps when lamellibranchs are feeding. Lotsy (1895), Moore and Pope (1910), Grave (1916), Martin (1923, 1927, 1928), Allen (1914, 1921), Coe (1948), Loosanoff (1949, 1950), Loosanoff and Engle (1947a,b), Loosanoff and Tomers (1948), and Nelson (1923a,b) have published papers dealing with feeding in various species of oysters and other lamellibranchs. Loosanoff (1949) found definite proof that *C. virginica* exercises selectivity in the type of food that it retains. He found that this species, when fed suspensions of algae of two colors, rejected one and swallowed the other. The algae which were accepted were no smaller than those rejected.

It has been reported in the literature that diatoms make up the principal food of the oyster (Lotsy, 1893; Churchill, 1921; Savage, 1925; and many other publications, both scientific and popular). The stomach contents of the oysters were examined and usually the silicious shells of diatoms were found in great numbers. But Martin (1923, 1927, 1928) stated that nanno-plankton forms (less than 25 micra in diameter) constituted 80–90% of the food. Later Coe (1948), Korringa (1952), and Hewatt (1952) have indicated that nanno-plankton and dissolved materials make an important part of the diet of oysters and other lamellibranchs. Churchill (1916) indicated the importance of absorption in the nutrition of the fresh-water mussel.

Observations and Experiments

1. SENSITIVITY OF O. EQUESTRIS AND C. VIRGINICA

It was noted early in the investigation that *C. virginica* had more frequent muscular contractions than *O. equestris; i.e.,* there were more shell movements. No special apparatus was used to count the shell movements such as was described by Nelson (1921b), Galtsoff (1926, 1928a,b), Hopkins (1931, 1933), Orton (1935), and many others. However, when both species were observed in filtered sea water under magnification, *O. equestris* remained open, the cilia on the mantle, gills and palps were active, and the adductor muscle was relaxed as long as five minutes at a time. On the other hand, *C. virginica,* even in filtered sea water, had a partial or complete contraction every minute or so. Often this species remained closed for five minutes or longer when there were suspended particles in the dish. *O. equestris* rarely remained closed for such long periods.

2. NANNO-PLANKTON AS FOOD

In the study with suspensions of plankton, no attempt was made to identify the organisms or even to measure their size. As would be expected, larger oysters were able to swallow slightly larger particles than smaller oysters. It has been mentioned previously that oysters utilize nanno-plankton. Several observations were made that support this. On several occasions in *C. virginica,* the mantle was so contracted that the tentacles acted as a screen to prevent the entrance of any particles visible under 100X magnification, yet a small mass of mucus formed at the apex of the palps and was swallowed. In two cases 430X magnification was used when this was observed, and though small specks were seen in the mucus ball, no organisms could be distinguished. Usually when the muscle was partially contracted and the mantle screened the passage of large particles, the activity of the cilia on the gills and palps continued at a constant rate, as though the animal were rapidly pumping water. This type of behavior was seen only in *C. virginica.*

3. LOCATION OF THE INHALENT REGION

Orton (1912) and Yonge (1926) have found that the particles are swept inward by the inbeating lateral cilia on the gill filaments, and that the particles usually enter over an area about 3 cm. wide in large oysters. The most common region of entrance (Figs. 12 and 15) is the posterior ventral region of the shell, called the incurrent canal by Nelson (1938). In the present investigation, in oysters less than about 1.5 mm. in shell length, carmine particles, detritus, and plankters have been seen to enter all along the ventral edge of the shell and even near the umbo anterior to the junction of the gills and palps. Though this occurred in both species, it was more common in *C. virginica* than in *O. equestris.* When this happened, the particles often went to the palps without first touching the gills.

4. FORMATION OF "PSEUDOSIPHONS"

On numerous occasions, especially if a heavy suspension was introduced into the dish, the right mantle was seen to contract so as to form a groove in the inhalent region. When this happened, particles entered only through this groove, since the mantle edges were contracted along the rest of the ventral edge. The formation of the "pseudosiphon" was rarely seen in oysters less than 5 mm. in length, although it was observed several times in oysters as small as 2 mm. The formation of the pseudosiphon was rarely seen in *O. equestris,* but it was a rather common occurrence in *C. virginica* of larger size, especially when there was a heavy concentration of particles in the surrounding water. Nelson (1938) discussed the phylogenetic significance of the pseudosiphon in relation to the adaptation of the *Crassostrea* type to silty waters. Nelson says that there are two exhalent siphons (pseudosiphons) formed by the contraction of the mantle in the exhalent region, the second being formed because of the promyal chamber (Figs. 12 and 13). In the present study, the two pseudosiphons were observed in *C. virginica,* but there was never more than one in *O. equestris.* The second pseudosiphon in the exhalent region was never seen in oysters less than about 5 mm. in length, which agrees with Nelson's statement that the promyal chamber is not developed until about one week after attachment. The pseudosiphon in the exhalent region was not seen as often as the one in the inhalent region, and it was never seen unless there was one in the inhalent region also.

5. PASSAGE OF PARTICLES ON THE GILLS

The particles that are brought into the mantle cavity touch the gills and are usually embedded in mucus. (MacGinitie, 1941, states that the mucus sheath on the gills strains the particles from the water that is brought in.) After contact with the gills, the particles pass anteriad to the palps. However, as mentioned above, particles brought into the mantle cavity along the anteroventral edge in very small oysters may go directly to the palps without first coming in contact with the gills. These particles in some cases move posteriorly and dorsally to the gills, joining others in the anterior movement to the palps. In oysters of the sizes used, the majority of the particles first come in contact with the gills about two-thirds of the way back (Figs. 12 and 13). In the smaller oysters, less than about 5 mm. in length, the majority of the particles travel on the distal or free margin of the gills, whereas in the larger oysters the movement of particles is more like that described by Nelson (1923a,b) and Yonge (1926). Part of the particles move along the ventral free edges of the gills and part dorsally in the grooves at the base of the gills. Carmine particles have been seen travelling both routes; this does not agree very well with the above investigators' findings that the larger particles remain on the groove of the ventral free edge and only the smaller particles go along the base. In oysters of the size used the majority of the particles that could be seen moved toward the palps along the ventral free edge of the gills. The particles move like a conveyor belt, and the passage is usually very rapid. In both species, particles have been seen on the palps within two seconds after they were put into the dish with the oyster. It was observed that the particles which moved along the base of the gills did not appear to be as heavily embedded in mucus as those along the free ventral edge (*i.e.*, they were more discrete). The former particles were seen most often in the larger oysters. The particles on the free ventral edge of the gills moved more slowly than those at the base and they were often overtaken and passed by the more discrete particles moving along the base.

According to Nelson (1923b) and Yonge (1926), the palps accept more of the particles which come from the base of the gills than of those from the free margin of the demibranchs. Although those along the free margin certainly seemed to be embedded in more mucus, this could never be verified or disproved, and small discrete particles were seen to enter directly into the esophagus from the basal grooves. Carmine particles of approximately equal size were used in the observations. In the larger oysters the particles could be seen travelling both routes, but mainly on the free ventral grooves. In the smaller oysters little if any of the carmine travelled the route at the base of the gills to the palps. Perhaps the gills do act as a selective mechanism in carrying the large particles along the ventral groove to the palps, which accept fewer of these than of the particles from the dorsal region. The more copious mucus on the ventral grooves tends to make the larger particles even larger and more likely to be rejected by the palps.

6. PALPS IN C. VIRGINICA

The palps (Fig. 17) of *C. virginica* are usually in close juxtaposition. Little material is accepted into the stomach without first going to the apex of the palps. Here the particles are revolved by ciliary action into a ball, called here a "food ball" even though it may not contain any food but only carmine or charcoal. However, small discrete particles sometimes leave the base of the gills, pass between the palps, and enter the stomach without first going to the apex of the palps. A considerable quantity of material of the size of nanno-plankton may have entered the stomach this way.

The mass at the apex of the palps is usually revolved clockwise to the axis of the body, although it has been observed to change directions and be revolved counter-clockwise. At the time that the mass is revolved it is rotated on its axis, so that it becomes rounded and more compact, judging from its size and opacity. If the food ball is of organic nature such as plankton, small particles break away, pass between the inner palps, and are swallowed. If the food ball is composed entirely of such things as carmine or charcoal, the small particles that break away are usually added to the revolving food ball again. If the mass is of the latter nature, the food ball is usually eliminated rather quickly as pseudofaeces. Sometimes, but rarely, if the food ball was composed of plankton and was small enough, the entire mass was observed to pass between the inner palps into the stomach. Usually more particles were added than were broken away, so that the food ball grew larger until it was eliminated as pseudofaeces.

It was extremely difficult to get *C. virginica* to accept pure suspensions of carmine or charcoal into the stomach. Even when carmine was mixed with plankton, the carmine was rejected as pseudofaeces along with most of the plankton. There was some sorting from the revolving food ball at the apex of the palps by the process previously described. In most cases the carmine or charcoal was rejected whereas some of the plankton was accepted. The particles that were accepted were sometimes larger than the rejected particles of carmine. On some occasions, carmine particles were swallowed after prolonged exposure to dense concentrations of this material, as if the inner palps had lost their sensitivity. Usually in cases of heavy feeding with carmine the mucus strands were seen to bunch at the base of the palps, proceed ventrad rather rapidly, and to be eliminated without revolving at the apex as food balls. Sometimes when an oyster had taken in large quantities of material, the heavy mucus strands, with embedded particles, could be seen coming from the base as well as from the ventral free margin of the gills, and passing in a continuous stream along the posterior edge of the palps to a point near the apex and then to the pseudofaeces tract on the mantle.-Sometimes, if the food given the oyster was plankton, a minute portion of small discrete particles went between the palps and was swallowed; but when the oyster had taken in a large quantity of plankton the palps were almost always pressed close together, and then all the mass was eliminated. It is not known how much unseen nanno-plankton went to the stomach. But these observations bear out the claim of Loosanoff and Engle (1947a,b) that oysters may lose weight in heavy concentrations of organisms.

The inner palps seem to have final choice of whether the particles are accepted or rejected. The exception to this is in the very heavy concentration described above, in which the particles are rejected without coming into contact with the inner palps. In *C. virginica,* with moderate concentrations of particles, some of the smaller particles were usually readily accepted by the inner palps and passed into the stomach, while the remainder, which entered the posterior edge of the outer palps, were carried to the apex and revolved as has been described. The particles that were broken away were either accepted or rejected by the palps. Sometimes the entire food ball went to the inner palps, in which case a rather violent lateral contraction of the inner palps caused the entire mass to be shot out as pseudofaeces.

7. PALPS IN O. EQUESTRIS

It has been stated above that *C. virginica* is selective as to what particles are swallowed. *O. equestris* seldom rejects anything of small enough size to enter the mouth and esophagus; it accepts indiscriminately carmine, charcoal, plankton, detritus, and silt. *O. equestris* will reject pseudofaeces, but only after the stomach, esophagus, and even the groove between the inner palps have become full. When this happens, there is a lateral contraction of the palps, and the mucus strand is regurgitated. At first there could be seen an elongated mucus string the shape of the groove embedded with particles, but ciliary action had already started to ball it before it got to the apex.

If small enough, the first particles that are brought to the palps by the ciliary action on the gills are readily accepted into the stomach by the palps without much revolving at the apex of the outer palps. It is only after the stomach has become full that there is much food ball formation. When the stomach and esophagus are full and the inner palps regurgitate the mucus string, additional particles from the gills bunch at the anterior end of the gills and are carried to the apex of the palps. This mass is incorporated into the food ball which is being formed from the regurgitated mass. While this is happening, the stomach is emptying rather rapidly (probably due to the food-sorting caecum described by Yonge, 1926, and Chestnut, 1950), and additional particles are swallowed. These may come directly from the gills or from the food ball. Discrete particles are added to the food ball also. Because of the rapid movement, it was difficult to determine whether the discrete particles that were added were ones that had broken away from the food ball or were new particles from the gills. However, the size of the revolving food ball decreases all the time, partly because some particles break away from it and partly because it becomes more compact due to the continual revolving and rotation. After the food ball has become smaller, there is a lateral contraction of the outer palps and the food ball comes in contact with the inner palps. Often the ball is swallowed. If not, there is another rather violent contraction of the palps, similar to that in *C. virginica,* and the mass is eliminated as pseudofaeces.

Food balls are formed also when larger particles and masses are carried at once to the apex of the palps and revolved there. Small particles are broken away, as in *C. virginica,* but no selection by the inner palps was ever seen. Carmine particles are readily accepted by the inner palps and passed into the esophagus if it is not already full. Meanwhile more particles are being added to the revolving ball, and if it reaches a larger size it is rejected as pseudofaeces.

8. PSEUDOFAECES TRACT

The rejection of the masses as pseudofaeces was different in the two species, as was their fate. The ciliated tract on the mantle (Figs. 12, 13, 15 and 16) is slightly different in the two species, but in both it is near the ventral edge of the mantle. The exit is slightly anterior to the principal entrance in *C. virginica,* but it is posterior and slightly dorsal to the inhalent region of *O. equestris.*

The oysters were observed through the left valve, and the pseudofaeces always followed the right mantle rather closely. It first was thought that this might be due to gravity, but when the oysters were viewed with the right side uppermost, the pseudofaeces still followed closely the inner surface of the right mantle. The figures (Figs. 15 and 16) show the ciliated tract on the right mantle, not on the left. It was common to see pseudofaeces travelling outward or toward the exit, while at the same time other particles were being swept inward. In the case of *O. equestris,* there was an actual crossover of the outgoing mass of pseudofaeces and the incoming particles. However, it was never observed that the current created by the gills for incoming particles ever caused the mass of pseudofaeces to return to the gills after it had approached the posterior periphery. Possibly the pseudofaeces were so bound in mucus that the ciliary tract in the mantle prevented them from being swept inward again. (A drawing, Fig. 14, of a frontal view of *O. equestris* shows a fold in the right mantle that has been tentatively identified as the pseudofaeces tract.)

Once the pseudofaecal mass is delivered to the pseudofaeces tract by the palps in *C. virginica,* it moves rather rapidly posteriorly (though not so rapid as the incoming particles), makes the right angle turn indicated in Figure 16, and goes to the border of the mantle. In a 5 mm. specimen, with about 2.5 mm. of pseudofaeces tract to travel, it took about two seconds for the pseudofaeces to move from the palps to the edge of the mantle.

In *O. equestris,* the mass rejected as pseudofaeces was usually returned to the palps several times. This was probably because the gills are more rounded ventrally, and are in closer proximity to the pseudofaeces tract in *O. equestris* than they are in *C. virginica* (Fig. 13). The combined inbeat of the cilia on the gills evidently causes a much stronger current than the outbeat movement on the tract, at least in the anterior half, where the two are in close proximity. Nelson (1946) discusses the movement of embryos within the epibranchial chamber and the path is similar to the movement of pseudofaeces described above.

The following observation illustrates the above. After an *O. equestris* 7.4 mm. in length and 7.1 mm. in height had been feeding on a pipettefull of plankton introduced six minutes previously, all intake of particles had stopped so far as could be seen. The larger particles had settled to the bottom of the dish and all the visible particles that remained in suspension had been ingested. At the end of eight minutes, all of the food that had been brought in had either been swallowed or had been rejected (two food balls) as pseudofaeces, except for one food ball which was being revolved at the apex of the outer palps. A few small particles were broken away and swallowed. A few small particles which had broken away from the food ball, and the larger ones that had become separated, later rejoined the revolving mass. The ball was becoming smaller, and the outer palps allowed the ball to pass to the inner palps. The inner palps pulsated laterally, and the ball was rejected to the pseudofaecal tract. During this process, several small particles became detached and were swallowed. The pseudofaecal mass travelled along the tract to a point about one-third of the way back (Fig. 15) where it was taken from the tract by the cilia on the gills and was again carried to the palps. The mass was carried to the apex of the outer palps and revolved; it was too large to be ingested directly. As the mass was revolved, becoming more compact again (it had lost some of its compactness because of the action on the gills where it followed the ventral groove in a mucus string), particles were either broken off and swallowed, or were reunited with the food ball. There was another pulsation of the palps, and then a rather violent closure, and the ball was again rejected as pseudofaeces. On the next trip back to the palps, via the gills, about the same procedure was repeated, except that one mass of particles that had become detached from the larger mass was accepted into the mouth by the palps, which had a slight lateral pulsation. The main mass was revolved at the apex and again, when passed to the inner palps, there was a pulsation and the mass was rejected. On the next trip back, after the third rejection, there were three lateral pulsations of the palps before the mass was finally rejected. During this passage, as before, some particles that were broken off were swallowed and some were reunited to the food ball before it was rejected as pseudofaeces. On the last trip (after the ball had been rejected four times and become much smaller), the palps opened and closed once in a pulsating movement and the entire mass was swallowed without first going to the apex. The series of trips from the first rejection to the final ingestion took four minutes and twenty seconds. Other such rejections and returns have been witnessed, and sometimes the food ball returned as many as six times before it was finally accepted into the mouth or rejected to the outside of the shell as pseudofaeces.

9. SHELL MOVEMENT

In order to eliminate the pseudofaeces which collects on the periphery of the mantle, both species snap the valves of the shell together by a quick contraction of the adductor muscle. In the position with the right valve undermost, *C. virginica* could eliminate the pseudofaeces beyond the edge of the mantle by ciliary action alone. However, during heavy feeding with consequent formation of large amounts of pseudofaeces, there were snappings of the shell which forcibly eliminated the rejected material. In *O. equestris*, the pseudofaeces were eliminated in almost every instance from the shell by a contraction of the adductor muscle. Usually two or three masses of pseudofaeces accumulated on the edge of the mantle before the adductor muscle contracted and closed the shell. Even then, the pseudofaeces were not expelled with much force; they often adhered to the edge and were sometimes brought back in with other suspended particles. The re-entry of pseudofaeces into the shell was never seen in *C. virginica.* Observations made on both species have shown that more effort is expended, and it is more difficult to expell the pseudofaeces, when the oysters are lying with the right valve uppermost than when the left or attached valve is uppermost. Nelson (1921a, 1938) and Hopkins (1935a), who discuss the attachment of spat, conclude that the natural position for the attachment of spat is on the under surface, and hence the left valve should normally be uppermost.

Movement of Particles in Intestinal Tract

The data given below were obtained incidentally during observations on feeding and are not considered conclusive. The passage of particles through the intestinal tract was timed in specimens of both species. The use of a carmine suspension was satisfactory with *O. equestris,* but *C. virginica* usually rejected this type of "food." However, it was possible to get *C. virginica* to accept some carmine by mixing it with plankton, and after repeated feedings with carmine this species would accept some. (Loosanoff, 1949, had previously reported that after several days *C. virginica* would accept food which it had previously rejected.) The most successful means of tracing and timing the passage of food in the alimentary tract of *C. virginica* was to stain plankton with neutral red as a "marker."

After entry into the mantle chamber, the passage on the gills to the palps is very rapid. In one observation of *C. virginica,* the particles (stained plankton) were at the palps within 5 seconds, and were seen in the stomach within 40 seconds. The stained material was seen in the intestine in one minute, and colored material was defecated in 16 minutes. The oyster on which these observations were made measured 12.0 mm. in length and 10.6 mm. in height. On another feeding of the same oyster, with carmine particles mixed with plankton, the carmine was seen in the stomach within 15 seconds and at the posterior loop of the intestine at the posterior edge of the digestive gland in five and a half minutes from time of feeding. The animal was defecating particles within eight minutes. Another feeding with carmine and plankton mixture had even faster passage. The carmine particles were in the stomach within eight seconds and were defecated in six and a half minutes. A feeding of stained plankton showed plankton in the stomach within fifteen seconds and defecation of stained faeces within ten minutes. Other observations on *C. virginica* showed about the same rate of passage of particles in the alimentary tract. Carmine particles consistently moved out of the stomach faster than did the plankton. This faster movement may have been due to the sorting device in the stomach which was described by Yonge (1926) and Chestnut (1950).

O. equestris ingested carmine readily, and the rate of passage of carmine particles was readily observed. The particles moved through the alimentary tract at about the same rate as in *C. virginica.* A few observations were made with stained plankton, which seemed to stay in the stomach longer than did the carmine, but too few observations were made to permit definite conclusions.

Carmine particles entered the stomach (based on observations of *O. equestris*) bound in mucus. There was much revolving and churning of the mass in the stomach, and the material left as more or less discrete particles. Whether this is due to the action of the crystalline style, as Nelson (1918, 1925b) contends, was not determined.

Material from the stomach collected in the upper portion of the intestine in a slow but rather steady stream. Peristaltic waves were seen to pass along the lower part of the intestine from about the region just posterior to the pericardial cavity. Material collected in the loop of the intestine until it reached this region and then progressed quickly to the posterior part. Faecal material would again collect in the posterior half of that portion of the lower intestine running from the posterior edge of the adductor muscle to the anus; this region acted as a rectum. The region of the intestine from anterior to the pericardial cavity to the rectal portion usually was clear of material, although on occasion the entire intestine was filled, especially if the oysters were closed. Defecation was often frequent but it did not empty the rectum as fast as new material accumulated, so there usually were faeces in the lower end of the gut.

Figures 19 and 20, camera lucida drawings of the posterior end of the intestine, show the large cilia found in oysters of both species when they are under about 5–6 mm. in length. These cilia normally pointed at right angles to the lower end of the intestine. They were seen to vibrate slightly as if a current of water were flowing past them. A solution of neutral red was given the oysters, but no current could be detected. When the animal defecated, there was a pulsation at the tip of the anus and the faeces were eliminated as pellets. When this happened, the cilia at the tip pointed straight posteriorly with their tips vibrating slightly, and seemed to act as an extension of the anus.

The elimination of faeces from the intestine was observed only when the oysters were active and the heart was beating, although the faeces were often trapped in the mantle cavity by closure of the shell before final elimination occurred. Material moved in the intestine down to the rectal region even when the adductor muscle was contracted. It is common to observe a full intestine in adult oysters that have been out of the water for some time. Often phagocytes could be seen moving in the walls of the intestine; however, it was not determined whether these cells were absorbing any material. The pellets of faeces sometimes were emitted at the rate of one every second when the oysters were active and a quantity of food was taken in. Not enough observations were made to determine whether the species differ in the action of the alimentary tract.

Elimination of Faeces in Exhalent Region

In oysters more than about 5 mm. long, in both species, the faecal pellets usually passed dorsad and slightly posteriad from the anus; this movement was rather rapid. Often in *C. virginica* a pseudosiphon formed in the region where the faeces were expelled and sometimes there were two (Fig. 13). When this occurred, the faecal material was expelled from the more dorsal and anterior one. The exit of the faeces was more rapid when a pseudosiphon was formed. *C. virginica* usually had a quick partial contraction of the adductor muscle which eliminated with some force the faecal material that had collected on the edge of the mantle or near the edge. *O. equestris* did not eliminate the faeces with as much force as did *C. virginica,* and the partial snapping of the shell was not as apparent in the former species. In *O. equestris* the faeces that sometimes remained on the edge of the mantle were brought ventrad and into the inhalent region along with other suspended matter, and accepted again as food.

Evidently the coordination of the cilia was not developed so well in the region of the exhalent chamber in small oysters under about 5 mm. long as it was in larger ones. Instead of following the usual path to the exterior, the faeces often were carried posteriorly to the base of the gills or to a position dorsad to the mouth. Sometimes the faeces remained within the dorsal mantle cavity as long as three minutes, in constant motion, before being ejected. The erratic ciliary action in a small *C. virginica* is shown in Figure 13.

Summary and Discussion

The main points of contrast in feeding behavior between the two species may be summarized as follows:

1. *O. equestris,* in contrast to *C. virginica,* remains relaxed (*i.e.,* open) and pumps water continuously for long periods. In *O. equestris* there is an almost immediate relaxation after contraction of the adductor muscle and closure of the shell, whereas the muscle of *C. virginica* will remain contracted, with the valves closed, for long periods, especially in turbid water.
2. In water of high turbidity the edges of the mantle so contract that the tentacles intermesh to "screen" out the larger particles. This was common in *C. virginica,* infrequent in *O. equestris.*
3. The formation of pseudosiphons in water of high turbidity was usual in *C. virginica,* especially the inhalent region, but rare in *O. equestris.* This is correlated with the function of the promyal chamber.
4. There is little or no pseudofaeces formation in *O. equestris* until the stomach and esophagus become gorged, unless the particles taken into the inhalent region are too large to be swallowed. *C. virginica,* on the other hand, forms copious pseudofaeces, especially in water of high turbidity.
5. The outer and inner palps of *O. equestris* accept any particles small enough to enter the mouth. The palps, especially the inner ones, of *C. virginica,* exercise great discrimination as to what particles are accepted.
6. Food balls formed at the apex of the palps are revolved longer, more particles are broken away and swallowed, and more attempts are made to swallow the entire mass in *O. equestris* than in *C. virginica.* It is by this process that *C. virginica* seems to select which particles are to be accepted and which are to be rejected as pseudofaeces. In *C. virginica,* the nature rather than the size of the particles appears to determine their acceptance, whereas in *O. equestris* any particles small enough to enter the mouth are accepted.
7. Pseudofaeces delivered to the mantle by the palps in *O. equestris* commonly return via the gills to the mantle, and the mass may be swallowed. Return of the pseudofaeces to the palps was never seen in *C. virginica.*
8. There is a better elimination of pseudofaeces to the exterior of the mantle in *C. virginica* than in *O. equestris.* Sometimes the pseudofaeces are carried to the edge of the mantle in *O. equestris* and then brought back into the incurrent region. This is asso-

ciated with the location of the exit of the pseudofaeces in the two species. In *C. virginica* the exit point is more anterior and ventral to the main incurrent region, whereas in *O. equestris* it is in a position slightly dorsal to, but almost in the path of, the incurrent region. Better coordinated or stronger ciliary activity, or both, in the pseudofaecal tract of *C. virginica* may also help account for this phenomenon.

9. There is also better elimination of faeces in *C. virginica* than in *O. equestris.* On occasions, faeces returned to the palps in the latter species, but this was never seen in *C. virginica.*

10. The gills are less important as selective organs than has previously been claimed. However, in larger specimens of both species some selection by the gills was seen; particles carried to the mouth at the base of the gills seemed to be more readily accepted than those at the ventral free edge. In the smaller oysters, all of the visible particles travelled along the ventral edge of the gills. In the very small oysters, particles were seen to contact the palps and be swallowed or rejected without first having been in contact with the gills.

The *Crassostrea* type, represented by *C. virginica,* seems to be more highly evolved in its ability to select food and also in its efficiency in eliminating waste material, pseudofaeces as well as faeces. The inner palps, especially in *C. virginica,* exercise the greatest discriminatory powers in food selection. The mantle, through the tentacles along the margin, acts as an initial selector by excluding the larger particles. The gills act as selectors in larger oysters, at least, in that the larger particles least likely to be used as food are consigned to the ventral edges, where they are less likely to enter the mouth.

The selection of food by the sensitivity of the organs mentioned above has disadvantages as well as advantages. Thus *C. virginica* may close the shell and not take in anything in case of high turbidity, or it may eliminate all particles (except possibly those of very small size) as pseudofaeces. *O. equestris,* on the other hand, eliminates nothing small enough to enter the mouth. Hence energy is expended, in this species, in ingesting and passing through the digestive tract particles which have no nutritive value.

CILIARY ACTIVITY

Introduction

There is ciliary activity in most tissues of the body of an oyster, especially those concerned with the passage of food and water. The role of the cilia in the feeding process and in the elimination of waste matter has been discussed above. In this section, the cilia themselves are considered in more detail.

Cilia on the Mantle

Figures 15 and 16 show the pseudofaecal tract of the two species. Figure 13 shows the paths of particles in the branchial and suprabranchial chambers of the mantle of small *C. virginica* (observed under 100X magnification). This is a composite diagram of several specimens of *C. virginica.* The number of arrows indicates the relative activity of each area. The movement was more irregular in the suprabranchial chamber. A similar activity occurred in *O. equestris,* but it was perhaps more erratic. Larger specimens of both species showed more coordination of ciliary activity.

There was an intense ciliary action along the periphery of the mantle (most noticeable in the inhalent region) in small specimens of both species. In small *O. equestris* a rather strong beat also occurs along the posterior dorsal region, which often moves eliminated faeces ventrad into the incurrent flow of water.

Both faeces and pseudofaeces are eliminated more effectively in *C. virginica* than in *O. equestris*. Often pseudofaeces, and sometimes even faeces, are returned to the palps in the latter, but not in the former. This suggests that the action of the outward-beating cilia is stronger, or better coordinated, or both, in *C. virginica.*

Cilia on the Gills

The action of cilia on the gills was reviewed and described by Yonge (1926). The present investigation was concerned mainly with the effect of temperature on them.

The contraction of the adductor muscle and closure of the oyster causes the cilia on the gills to cease beating. It appeared, from observations made at room temperatures, that the cilia on the anterior end of the gills were the last to stop beating when the oyster closed, and the first to start when the oyster opened again, while those along the free ventral edge were the first to stop and the last to start. However, at room temperature these changes were so abrupt that precise observations could not be made.

An apparatus was devised (described on page 82) by which the temperature could be lowered or raised at a slow and relatively uniform rate. By use of this device, the cessation and initiation of ciliary beat were slowed considerably, so that more nearly accurate observations could be made. Preliminary experiments indicated that the sequence of ciliary activity as the temperature was lowered and then raised again was the same as the apparent sequence in contraction followed by relaxation. By way of example, one such experiment is described below.

A specimen of *O. equestris* attached to a glass slide had been brought from Port Aransas to College Station on July 28, 1952. It was stored in sea water in an ice box at a temperature range of 5–8° C. until July 31, 1952, when the slide was set up with the temperature regulator and allowed to warm gradually to room temperature. This oyster measured 1.0 mm. in diameter, and the gill was composed of one lamella only of the right and left demibranch. The left demibranch was more developed than the right, and, because it was uppermost, observations were made on it alone. There were 21 filaments with cilia; one additional filament was only a nodule with no cilia. The posterior five or six filaments were much less developed than the anterior ones, the last two cilia-bearing filaments being only about one-fifth as long as the more "normal" anterior ones. The shell was broken slightly at the attachment of the adductor muscle to the left valve, so that the oyster could not close tightly. It has been noticed repeatedly that the cilia on the gills are constantly in action if a valve is removed or broken, regardless of contraction of the adductor muscle, the mantle, or the gills themselves. The apparatus was set in operation at 8:45 A.M. Observations were started at 8:55 A.M. and continued at one minute intervals from 9:00 to 10:15 A.M., and then, after 30 minutes rest, at from one to five minute intervals from 10:45 A.M. to the termination of the experiment at 12:00 noon.

The data, as originally taken, included the temperature change for each observation (Table XXVII). Observations were also made on the ciliary activity of the style sac and in the stomach.

It is seen from the log (Table XXVII) that a progressive decrease in ciliary movements on the filaments from the posterior to the anterior occurred when the temperature was lowered. After ciliary movement ceased at the distal end of the filament, it sometimes persisted at the basal portion until the temperature was several degrees lower. When the temperature was raised, the cilia at the base of the filament usually resumed activity at a temperature several degrees lower than those at the distal end.

The log shows only whether cilia were moving, not the degree of movement. In a decreasing temperature, the ciliary movement slowed gradually before ceasing alto-

TABLE XXVII

Log of Ciliary Activity of O. Equestris Under Temperature Control.
(Gill Observations on Single Left Lamella of 21 Filaments)

		Lamella			
		Cilia Movement Ant. Filaments		Ciliary Movement	
Time (A.M.)	Temp. C.	Entire	Base Only	Style	Stomach
8:55	19.0	21	0	Present	Present
9:00	18.0	21	0	do	do
9:01– 9:04	17.5–16.0	19	2	do	do
9:05– 9:11	15.5–12.5	16	3	do	do
9:12– 9:16	12.0–10.8	16	2	do	do
9:17– 9:18	10.5–10.2	15	0	do	do
9:19	10.0	14	1	do	do
9:20– 9:29	10.0–8.7	14	0	do	do
9:30	8.6	13	1	do	do
9:31	8.5	10	1	do	do
9:32	8.4	6	2	do	do
9:33– 9:34	8.2	6	0	do	do
9:35	8.1	2	1	do	do
9:36– 9:48	8.1–5.0	2	0	do	do
9:49	4.0	2	0	do	Absent
9:50–10:02	3.0–1.0	2	0	do	do
10:03	0.8	1	0	do	do
10:04	0.7	0	0	do	do
10:05–10:12	0.7–0.0	0	0	Absent	do
10:13	-0.9	0	0	do	do
10:14–10:15	0.0	0	0	do	do
(Observations discontinued until 10:45 A.M.)					
10:45	4.5	0	1	Present	Absent
10:49–10:51	5.0–5.5	1	0	do	do
10:53	6.0	2	0	do	do
10:54	6.2	5	1	do	do
10:55–11:00	6.5–7.0	6	0	do	do
11:02	7.2	7	0	do	do
11:03	7.5	8	0	do	do
11:04	7.8	8	1	do	do
11:05–11:07	8.0–8.5	9	0	do	do
11:08	8.6	9	0	do	Present
11:10	9.0	9	1	do	do
11:12	9.1	10	0	do	do
11:14	9.3	10	1	do	do
11:15–11:32	9.5–11.0	11	0	do	do
11:34–11:35	11.2–11.5	11	2	do	do
11:37	11.8	11	4	do	do
11:38	12.0	12	3	do	do
11:40	12.2	14	2	do	do
11:42–11:50	12.6–13.5	16	3	do	do
11:52	14.5	19	1	do	do
11:55–12:00	15.0–16.0	21	0	do	do

(When observations terminated, cilia beat as rapidly as at start of experiment.)

gether. However, in the series of observations in which the temperature was raised, the ciliary movement was not resumed gradually, but abruptly and rapidly after a certain threshold was reached. This phenomenon was also noticed in oysters that contracted at room temperature (25° C.±). When the oyster contracted there was a gradual stopping of the ciliary beat on the gill filaments, but upon relaxation the commencement of ciliary activity was instantaneous.

Galtsoff (1928a,b) found that the optimum temperature for ciliary beat on the gills in *C. virginica* was between 25 and 30° C., and that below 5° C. no current was produced although the cilia continued beating until the freezing temperature of sea water was reached. He stated that the lack of current below 5° C. was due to lack of coordination of the ciliary motion along the surface of the gill. Hopkins (1933, 1935b) found in *C. gigas* that the optimum temperature for feeding was about 20° C., whereas the optimum for pumping activity of the gills was about 27° C. to 28° C. Hopkins (1931) reported that *O. lurida* underwent a hibernation in respect to gill activity between 4° C. and 6° C. and that it was extremely sensitive to temperature changes at the lower ranges, whereas changes above 17° C. produced little change of activity in this species. Loosanoff (1950) found that *C. virginica* could pump water at temperatures below 3° C. The rate of pumping steadily increased in the range from 8° C. to 16° C., with a rather constant rate of pumping from 16° C. to about 28° C.

Although the present experiments were preliminary and not extensive, they may explain why oysters show a decrease in pumping at lowered temperatures. It is not only a slowing of the ciliary beat but an actual stopping of all movement in a progression from the posterior to the anterior filaments of the lamellae. More observations need to be made, especially on larger oysters, which may not behave exactly the same as small specimens with incompletely developed gills.

Cilia on the Palps

The ciliary activity of the palps has been discussed in the section on feeding, but a few more observations are given here. It was observed on numerous occasions that the cilia on the palps continued movement after the adductor muscle had contracted and after the cilia on the gills had stopped beating. However, the movement lasted for only a short time, usually less than two minutes, if the oysters remained closed tightly. The food ball continued to revolve, at least in *O. equestris* (no specific observations were made on *C. virginica*), if the adductor muscle contracted while such a process was being carried on, even after ciliary activity had stopped in the gills. In fact, food balls were often accepted into the mouth or rejected after the shell had closed.

The observations in which the temperature was decreased revealed that the cilia continued movement on the palps to a temperature below about 3° C., but it was very slow. Ciliary movement in these organs showed a noticeable progressive decrease below about 8° C. Any change of ciliary movement which occurred at high temperatures could not be discerned because of the rapidity of the movement. In one observation on *O. equestris*, some particles were carried to the palps by the gills at a temperature of 8.2° C. The ciliary activity had become noticeably slower but when the food reached the palps there was an immediate increase in activity. Whether or not increased activity of cilia is stimulated by contact with particles at higher temperatures is not known. However, there was usually an overall increase in activity of the palps, indicated by more frequent lateral pulsations, when particles were present.

Cilia on Esophagus and Stomach

On numerous occasions ciliary movement was seen in the esophagus. Particles entering the mouth moved quickly to the stomach and no peristaltic movement of the esophagus was ever seen. Yonge (1926) pictures the esophagus with relatively short cilia.

There was an almost continuous movement of particles in the stomach. This movement was seen easily unless the stomach was so full that it was rendered opaque. Cilia were seen moving in the stomach after the adductor muscle had contracted and the shell had closed. Yonge (1926) says that most of the movement in the stomach is caused by the rotation of the style, and he and Nelson (1918, 1925b) found that one of the chief functions of the style is to stir and mix particles in the stomach. These investigators had found that the style rotates in a clockwise movement, and this was verified by the writer. Also there was an overall clockwise movement of particles, although some movement was counter-clockwise. In explaining the reverse movement, Yonge (1926) says that a ciliated ridge in the caecum sorts the heavy particles to one side. These heavy particles then pass to the mid-gut and the lighter ones go to the gastric shield.

Yonge (1926) said that the style revolved 60 to 70 times per minute. In the present investigation, it was found that the speed varied from about five per minute at temperatures as low as 5° C. to 75 revolutions per minute at 28°–30° C. Cilia in the style sac moved at much lower temperatures than did the other cilia in the stomach (Table XXVII) and there was still slight movement at 1.0° C. According to the data in Table XXVII and other observations, the minimum temperature for activity of the cilia in the style sac was about four degrees lower than the minimum for activity of cilia in other parts of the stomach.

Summary and Discussion

Ciliary action in the various tissues of the oysters is described. Some of these observations corroborate previous findings. It was found, as had been mentioned in the preceding section, that the ciliary activity of *C. virginica* was much stronger and better coordinated than that of *O. equestris*. It was found that the ciliary action as indicated by movement of particles in the mantle cavity, especially the suprabranchial chamber, was erratic and uncoordinated in small oysters. As the oysters became larger, movement of the particles became less erratic.

Preliminary observations on the effect of temperature on ciliary movement indicated that ciliary activity on the gills diminished in almost geometric progression as the temperature decreased. The beat of the cilia themselves became slower, and also the ciliary activity of filaments from anterior to posterior was correlated with changing temperatures. Thus at low temperatures the cilia on entire filaments of the gills at the posterior end ceased beating. Also, as the temperature was decreased a progressive cessation of entire filaments toward the anterior end resulted. The cilia on the anterior filaments were the last to stop at lowered temperatures and the first to start when the temperature was raised again. The cilia at the base of each filament continued beating at a lower temperature than did those at the distal end. The slowing of the ciliary beat and the complete stoppage of the cilia on the filaments explains the decrease in amount of water pumped at lower temperatures.

The cilia on the palps continued activity at a low temperature; those on the gills, at a still lower temperature, but the movement was very slow. Ciliary movement on the palps continued after the oyster had closed and after ciliary activity had stopped on the gills.

The cilia in the style sac continued movement at temperatures lower than those at which cilia stopped in other parts of the stomach. These cilia in the style sac ceased beating at about the same temperature as those on the gills.

CONTRACTION IN MANTLE, GILLS, ADDUCTOR MUSCLE, AND HEART

Introduction

The technique of examining living oysters under the microscope afforded an opportunity to observe various other functions besides feeding. The following observations, incidental to the main study of feeding and ciliary activity in the two species, corroborate and augment some of the previous research on the several species of oysters.

Contraction in the Mantle

The contraction of the mantle has been discussed before rather fully and need only be reviewed here. The edges of the mantle normally extend to the edge of the shell when the animals are relaxed and active. In *O. equestris,* the mantle often extended beyond the edges of the shell in the small oysters used, whereas in *C. virginica* there was usually a partial contraction. It was mentioned above that in *C. virginica* the edges of the mantle often contract so that the tentacles intermesh and form a screen which keeps out larger particles, even though the animals are actively pumping and smaller particles enter. This phenomenon was rarely seen in *O. equestris;* in *C. virginica* it occurred most often when a heavy suspension of material was in the water.

In the smaller oysters of both species, the contraction of the mantle (as well as the gills) seemed to aid vascular movement. An almost continual contraction and relaxation of the mantle occurred in both species in individuals under about 5 mm. in shell length. Observations on oysters under 2.5 mm., before the heart had become active, revealed that partial contractions occurred about every five to ten seconds when the oysters were open and active. Usually when the mantle contracted, the left lobe did not contract as much as the right and was therefore further extended. Also, the right lobe was the one which puckered and formed the pseudosiphons.

The contractions of the mantle in relation to heart beat and adductor muscle contraction are discussed in a later section.

Contractions of the Gills

Like that of the mantle, the contraction of the gills aids in the vascular movement, especially in small oysters. Elsey (1935) states that the contraction of the gills can force blood into certain interfilamentar and interlamellar tissues.

The gills were usually tightly contracted when the shell was closed. In the smaller oysters, where all the lamellae and filaments had not developed, the contraction was so intense that the filaments were wavy instead of straight. This was seen in both species.

Contraction of Adductor Muscle

The contraction of the adductor muscle was discussed in the section on feeding. Some of the activities that continue or cease when the adductor muscle is contracted are included here.

It has been observed that the crystalline style revolved as long as five minutes after the adductor muscle was contracted and the shell was tightly closed. Often there was ciliary action on the palps after contraction of the adductor muscle.

Hopkins (1936c) studied the adductor muscle and made several observations which were confirmed in the present investigation. He used kymograph records of the opening and closing of the shell, and made a direct study of oysters which had attached to plane glass plates. He found that contractions of the adductor muscle, producing partial closure of the shell, fell into three classes. Water may be discharged from the inhalent chamber, the cloacal chamber, or both. He found a kind of rhythmic partial closure which resulted in expulsion from the cloacal chamber that was probably associated with the elimination of faeces. This was discussed previously. He found, as did Nelson (1921b, 1923a, b) and as was confirmed in the present investigation, that the most frequent contractions occurred when a heavy amount of suspended material was in the water.

Figures 21 and 22 are camera lucida drawings of the living muscle when contracted and when relaxed. The muscle was often contracted to various degrees, however, and many intergradations between the two conditions shown in the drawings were seen. The present investigation bears out Hopkins' statement that contraction is quick but relaxation is slow.

A contraction of the adductor muscle occurred whenever the light was reduced. This was apparent when the oysters were being viewed under magnification. The reaction is more pronounced in *C. virginica* than in *O. equestris.* In fact, the quick passage of the hand in front of the source of light caused a contraction of the adductor muscle, the mantle, and the gills in *C. virginica.* It was never determined which contracted first, the mantle, the gills, or the muscle. It took a rather drastic reduction of light to cause the muscle of *O. equestris* to contract. An increase of light had no effect even when the change in intensity was many times the magnitude of the decrease. Oysters of both species, after contraction, relaxed under reduced light intensity. Nelson (1938) found an absence of the "shading response" in the *Ostrea* type *(O. edulis)* and said that this was correlated with absence of pigment in the mantle. (*O. equestris* usually had some pigment in the border of the mantle, but much less than *C. virginica.*)

Heart Contraction

Owen, Maduell and Ingle (1949) devised an instrument that they thought would successfully record the heart beat in an oyster without removing one valve. They named the apparatus the "Ostreodynamometer," but as yet no report of the results obtained by its use has been seen. Takatsuki (1927, 1929, 1932) published on the effect of temperature on the contraction rate of isolated hearts of *O. circumpicta* Pilsbry. He found that the heart beat is completely stopped at 0° C., and resumes when the temperature is raised to from 5° C. to 7° C. He found that oysters that normally live in water of high temperatures were more sensitive to low temperatures than those that were normally cold water inhabitants. The reverse was also true. In some of his experiments the rate of heart beat for isolated hearts of adult oysters was 14 per minute at 20° C. and 30 per minute at 35° C. Hopkins (1936a) cut away the shell and observed the heart beat. He found a rate of about 18 times per minute at temperatures from 17° C. to 18.5° C. Prytherch (Higgins, 1931) observed that the heart beat of *C. virginica* stopped at temperatures of 2.5–5° C.

The observations on the small oysters gave some information on the heart beat. This information is given in Table XXVIII. Unfortunately, no observations were made at very low temperatures, and the majority were made on small oysters about 5 mm. long.

TABLE XXVIII

Rate of Heart Beat Per Minute

O. equestris				*C. virginica*			
	Size				Size		
Temp. °C.	Length (mm.)	Height (mm.)	Rate	Temp. °C.	Length (mm.)	Height (mm.)	Rate
17.0	5.0	4.1	30	25.0	4.4	4.0	100
18.0	5.4	5.1	75	27.9	4.4	4.0	105
20.0	5.0	4.1	80	28.0	4.4	3.6	100
21.3	5.4	5.1	80	28.0	4.0	3.6	105
22.0	5.4	5.1	85	28.0	8.4	8.3	140
22.5	5.4	5.1	80	28.0	12.0	12.0	105
22.5	5.0	4.1	75	28.0	16.5	14.0	105
23.0	5.4	5.1	85	28.0	15.0	14.6	135
24.0	5.0	4.1	80	28.4	2.5	2.5	95
26.0	5.0	4.1	75	29.0	8.0	7.2	105
28.5	3.0	3.9	85	29.0	4.1	3.7	130
28.5	6.6	6.3	105	29.0	5.4	5.4	135
28.5	6.6	6.3	120	29.8	2.5	2.5	80
29.0	6.6	6.3	135	29.8	3.5	3.4	125
29.0	3.5	3.3	135	30.1	2.4	2.1	95
30.0	7.2	7.0	135	......	....	....	....
32.4	11.5	10.5	125	......	....	....	....

A few tentative conclusions can be drawn from the data in Table XXVIII. In both species a progressive increase in rate of beat occurs up to about 30° C., but not above this temperature. Federighi (1929) found similar results. On the whole, there seemed to be a faster rate of pulsation in oysters over 5 mm. long than in those of smaller size.

In both species, a partial contraction of the mantle often had little effect on the heart beat. The heart was seen to beat even when the adductor muscle was partially contracted (though at a slower rate). Sometimes the heart would not beat even though there was ciliary activity and the animal was feeding actively. This does not mean that no flow of blood occurred, for the contractions of mantle, gills, and adductor muscle caused some vascular movement. In smaller oysters, the heart often beats spasmodically several times, then stopped for as long as two minutes, even though the shell was open and the animal was feeding.

An attempt was made to determine whether the beat of the heart forced blood into the sinuses of the mantle and gills to activate or "pump up" these organs after they had contracted, as suggested by Dr. Gordon Gunter of the Institute of Marine Science (personal communication). But no such indication was found. In fact, it was observed many times that when the oyster began to open again, after it had been stimulated to contract, the heart started beating several seconds after the adductor muscle and mantle had started to relax. After the importance of the contractions of the mantle and gills in vascular movement was ascertained, it was realized that it would be extremely difficult to evaluate the effect of vascular movement on relaxation after muscular contraction.

Accessory Hearts

Accessory hearts and pulsating blood vessels were observed in both species during the present investigation. The best observations were made on spat that had remained in aquaria for a week or more and were emaciated. When neutral red was placed in the container with the oyster, the phagocytes would take up the dye readily, allowing even better observations. Figure 25 is a camera lucida drawing of the accessory heart in the left mantle *(O. equestris)*, with some of the adjoining tissues. (The excretory organ can be seen adjacent and posterior to the adductor muscle.) When the accessory heart contracts, it does so as described by Hopkins (1934a,b, 1936a), with the blood moving distally to the circum-pallial vessel. This results in the entire diameter becoming smaller, and the posterior end seemingly closes entirely. No contraction was seen in the circum-pallial vessel, but when the posterior end of the accessory heart relaxed with an incoming surge of blood from its anterior end, the blood in this vessel was seen to flow back a short distance into the accessory heart. But the oncoming progressive contraction forced the blood back into the vessel in the periphery of the mantle. The blood flowed both dorsally and ventrally in the circum-pallial vessel.

The beat of the accessory heart is independent of the heart beat, as found by Hopkins (1934b). Hopkins used larger oysters than were used in the present study, and made his counts at lower temperatures, 17.0 to 18.5° C. Under these conditions, he found that the heart beat at the average rate of approximately 18 times per minute, while the accessory heart beat only 6.0 to 7.5 times per minute. In the present investigation, only small spat were observed, at temperatures ranging from 28.0 to 30.0° C.; under these conditions, the heart beat 100 to 125 times per minute, and the accessory heart beat 15 to 20 times per minute. Thus the rate of beat of the accessory heart was one-fourth to one-third that of the heart at 17.0 to 18.5° C., according to Hopkins, but this ratio was only one-eighth to one-fifth at 28.0 to 30.0° C. The accessory heart sometimes continues to pulsate when the heart is completely stopped, and also when the oyster is partially closed and the mantle is contracted.

Summary and Discussion

The contraction of the mantle in the feeding process and the formation of the pseudosiphons has been discussed above. The contraction of the mantle and the gills aided in vascular movement.

The contraction of the adductor muscle described in previous investigations were corroborated by the present observations. Most attention was given to the cessation of other functions when the muscle contracted. The heart beat stopped a short time after the shell closed, as did ciliary activity on the gills and other parts. It was found that individuals of *C. virginica* were much more sensitive to "shading" than individuals of *O. equestris*, and that an increase in light intensity had no apparent effect on muscular contraction.

Counts of the heart beat per unit of time were much higher than those recorded in previous investigations. However, Roughley (1933) states that small oysters have a much faster rate than larger ones. No correlation could be found between the contractions of the pulsating blood vessels (accessory hearts) in the mantle and contractions of the heart, although the former were slower. The rate of heart beat increased progressively at higher temperatures up to about 30° C., and then decreased slightly.

Discussion

The comparison of the two species of oysters, now placed in two genera, lent itself admirably to clarifying some of the controversies concerning certain phases of the biology of oysters. It is felt that certain details, which otherwise might have been overlooked, were seen by the direct comparison of the two under the same conditions. This was certainly true in the observations on the intake of food and the stratification of strike.

The use of the "glass" oyster, in which intact living oysters were observed under magnification, was deemed more satisfactory than the methods used in previous investigations in which the oysters were observed by removal of one valve, or through a window in the shell. The above method not only lent itself well to observation of the ciliary action, but it can also be used in many other problems of oyster biology. Details of the anatomy, *e.g.*, of the vascular system, can be studied in this way in the living condition. In pollution studies, the pollutant can be introduced and observations can be made directly on the physiological activities of the oysters. Observations on feeding, using this method, can be of importance in future oyster culture programs.

One handicap in the use of this technique is that it is limited to small oysters. It is not certain how the activities of the adult differ from those of the spat, but the indication is that they are not the same. Thus it was observed that the ciliary action in small spat was less coordinated than in those of larger size, and the heart beat is more rapid in smaller oysters than in larger ones. Perhaps all muscular contractions and ciliary activity become slower as the oysters become larger.

Some additional biological facts have been uncovered in this investigation. In fact, practically all that has been learned of the biology of *O. equestris* has been new because this species had not been investigated extensively before. The observations indicate, however, that it is similar to other species of the genus and hence can be considered representative of the genus *Ostrea.*

It was found in the life history studies that *O. equestris,* despite being a warm water inhabitant, had a lower minimum temperature threshold for the initiation of spawning than did *C. virginica.* It had been found before that *C. virginica* has several physiological races, occurring at different latitudes, which differ in regard to the critical temperature for spawning. In the warmer waters of the Gulf Coast of the United States, the critical temperature is 25° C. The genus *Ostrea* has been characterized as a cold water group, even though some species live in warm water. *Crassostrea,* on the other hand, is a warm water group, although some live in cold water and *C. virginica* can withstand freezing (*O. lurida* is killed by freezing). Even though it is a warm water species, *O. equestris* had an important phase of its life cycle, namely spawning, geared to cold water as is characteristic of the genus. It would be interesting to determine the critical temperature of spawning of other warm water species of *Ostrea.*

Several anatomical features have been found that warrant some discussion. The cilia on the tip of the anus apparently have not been described previously. These probably are the same as the anal cilia of the larvae, shown by previous investigations and the present study. The cilia persist for several weeks after attachment of the spat, and then disappear. It is not surprising that they have not been seen before. They were not noticed for some time in the present investigation and only then by their movement when defecation was studied in the "glass" oyster. There are at hand several permanent mounts of entire oysters that show them, but if they had not been seen in the living oysters, they could easily have been overlooked. An attempt to find them in sectioned material was unsuccessful.

The shell was studied to determine why a better observation could be made through the left valve than the right. It was readily apparent that the left valve was more satisfactory in the larger spat because of the diffuse chalky calcification that appeared earlier in the right valve. However, the smaller oysters have no chalky calcification in either valve, and it was thought at first that perhaps there was no periostracum or conchiolin material on the left valve. But when both valves were treated with acid and the remains were examined under magnification, it was found that both had conchiolin, but that it was different in the two valves. That of the right valve was "cellular-like," while that of the left was homogeneous and thus afforded better visibility. Preliminary experiments were performed in which portions of the right and left valves were removed. The oysters were then placed back in the water and allowed to repair the removed portions. The replaced shell was treated with acid and examined as before. It was found that the new conchiolin from the respective valves was the same as on the original. This would indicate that there is some difference in the secretion of the pallial lobes, but microscopic examination of prepared material revealed no histological differences between the two. The histology of the mantle deserves additional study.

The stratification in the setting of the two genera received much attention. In addition to the experiments performed in the present investigation, past observations and published data were used. The data followed a fairly consistent pattern. *O. equestris* occurs only in the saltier waters and most of the spat are found on or near the bottom below low tide level. *C. virginica* occurs in both the saltier waters and the brackish waters of estuaries. In the waters of high salinity this species attaches only near the surface or in the intertidal zone. In waters of low salinity, most of the setting occurs on or near the bottom, or subtidally. These respective patterns of attachment in relation to salinity are characteristic of the two genera, with few exceptions.

The intertidal occurrence of *C. virginica*, along the South Atlantic coast of the United States especially, has been explained by the abundance of enemies in the deeper waters that prevent their survival. In fact, there have been several reports that this species attaches near the bottom subtidally in waters of high salinity but that none of the spat survive to become adult (McDougall, 1943; Chestnut and Fahy, 1952, 1953). Two objections may be raised to these conclusions. The first is that although these investigations were conducted in areas where *O. equestris* is endemic, no attempt was made to identify *O. equestris* spat in the culch experiments, all spat being counted as *C. virginica*. Hence it is possible that the difference in stratification found at Port Aransas and Pensacola was also present, but undetected, in these experiments.

Secondly, if *C. virginica* attached in the numbers reported, it is difficult to believe that no individuals would survive to become adult. It is known that *C. virginica* can live on the bottom, subtidally, in waters of high salinity. The writer recalls an incident on the Seaside of the Eastern Shore of Virginia. Here all the natural reefs are intertidal, but some of the commercial oyster planters make a practice of planting oysters from these reefs in the small creeks in water from about two to twelve feet deep. One such planting was examined as the oysters were removed for sale. There was a mortality of about 30% caused by the oyster drill, *Urosalpinx cinerea* Say, but some of the intertidal reefs have been found that had a 99% mortality caused by this snail. The subtidal oysters appeared to be in excellent condition otherwise.

Several plausible hypotheses have been advanced to explain the pattern of attachment of individual species of both *Ostrea* and *Crassostrea.* But none of these seems satisfactory when the different behavior of the two genera, under the same conditions, is taken into account. It appears that the difference in setting must reflect intrinsic differences in the larvae of the two genera. Both types occur on the bottom in the salinities to which they are best adapted. *Ostrea* occurs only in waters of near oceanic salinity. The *Crassostrea* type occurs over a wide range but is seemingly betted adapted to the lower salinity levels. This fact suggests that the specific gravity of the larvae of this type is less than that of the *Ostrea* type. If this is true, *Crassostrea* larvae would tend to "float" in waters of high salinity. The larvae would have to swim actively in order to move out of the zone where the effect of such a physical relation would place them. Of course where there is a strong current or turbulence, the tendency would be to find setting of both types over a wider stratum than if such factors were absent. It should be possible to test this hypothesis experimentally.

Only a survey was made of the diseased and predators of oysters in the Port Aransas region. The relatively short life span of oysters in the area of high salinity at Port Aransas had been ascribed to the abundance of predators. Other investigators have stressed the high mortality caused by predators in the more saline waters, especially in the case of *C. virginica.* A high mortality in recently attached spat was found, which is similar to the findings in previous investigations. Competition with other sessile organisms and among the spat themselves has been one explanation offered for this high mortality. The present investigation on the feeding activities suggests another possible explanation. It was seen that a newly attached spat lacks coordinated ciliary activity and therefore cannot rid itself of waste materials as effectively as an older spat, especially in *C. virginica.* In this species, in fact, the promyal chamber does not develop until several weeks after attachment. The promyal chamber is an anatomical adaptation for living in turbid waters (Nelson, 1938). Thus the young spat have to contend with the same turbidity factors as older ones, with less adequate facilities to handle them. It is biologically probable that a high mortality would occur even if competition and predators were absent.

The results of the growth experiments showed that *C. virginica* attained a much larger size than did *O. equestris.* This latter species is generally a small oyster and does not reach a size large enough for commercial use in turbid bay waters. Specimens of *O. equestris* of much larger size were found, however, in the relatively clear waters of the Gulf of Mexico. The probable explanation for this is that in the turbid waters this species, which exercises no discrimination in its feeding, is at a disadvantage because such a small amount of the total material it takes into the stomach can be utilized as food. The explanation of the apparent equal growth rates of the two species for a short period after attachment is that given in the preceding paragraph; *i.e.*, the ciliary coordination of *C. virginica* is poor at first and no promyal chamber is formed until several weeks after setting. Hence both species would suffer from some of the same disadvantages during the first few weeks of sessile life.

Previous investigators of feeding in oysters have stated (1) that oysters are not selective in their feeding except as to particle size; and (2) that oysters are very selective, and will reject some particles which are smaller than those accepted. It was found that *O. equestris* conforms to the first statement, and *C. virginica* to the second. Past investigators have tried to reconcile the feeding habits of these two types of oysters because they were formerly placed in one genus.

The importance of the gills as selective organs, emphasized by Yonge (1926), was found by study of the "glass" oyster to be rather minor. In no case observed was material pushed from the gill to the mantle to be eliminated as pseudofaeces, as Yonge claimed. There was, however, especially in the larger spat, a strong indication that the gills were selective in one manner. Small particles, but no large ones, often travelled to the palps along the base of the gills, and these small particles were more readily accepted into the palps than were particles which came from the ventral free edge of the gills. This selectivity by the gills had been found by previous investigators.

McGinitie (1941) found that oysters do not feed unless there is a mucus film present on the gills. He concluded that oysters may be pumping water and still not feeding unless there is such a film. A contradiction of this observation was apparent when particles were seen to enter the mantle chamber, move to the palps, and be taken into the stomach without first coming in contact with the gills at all. It is true, however, that this phenomenon was seen only in the very small spat. Many investigators have emphasized the importance of the mucus on the gills to trap particles. From the present investigation, it seemed that the mucus impeded the passage of particles to the palps. It was seen that in very heavy feeding *C. virginica* rejected everything as pseudofaeces, and *O. equestris* seldom formed pseudofaeces unless there was heavy feeding. Perhaps the mucus film is an advantage in preventing too much food from reaching the palps at once and being rejected as pseudofaeces.

The activity of the palps in the two species upon contact with supended particles has been described. The cerebral ganglia are in close proximity to the labial palps, and these organs have a rich nerve supply. The rejection of particles by *C. virginica* has been described as a "sense of taste." But this sense must be through physical neuro-muscular reactions rather than chemical, because such things as charcoal, which is inert, are immediately rejected. But possibly there is some chemical neuro-muscular reaction also, because accidental feeding of this species with its own faeces on several occasions resulted in an immediate and rather violent rejection by the palps. *O. equestris* definitely seems to lack the chemical reactions, because it was observed on numerous occasions to feed on its own faeces. The rejection of pseudofaeces by the palps in this species occurred only after there was space for no more material in the stomach.

At first thought, it would seem to be a disadvantage for *C. virginica* to be so sensitive in its feeding habits. It was found that in the case of high turbidity, everything was rejected, with the possible exception of particles too small to be seen under the magnification used. But it is concluded from the observations of the smaller individuals of *O. equestris* in the more turbid areas that it is much more efficient to reject much of the nutritious material along with the non-nutritious, than to take in everything indiscriminately. The selectivity of *C. virginica* does work to a disadvantage in some cases, because past investigations have shown this species to be starving in a sea of plenty, so to speak, when the planktonic organisms were of such nature that they were rejected by the oysters. Yet this species lives and thrives in water of high turbidity, and probably it is able to do so only because of the selectivity in feeding.

It would be expected that the *Ostrea* type is more efficient in feeding in clear oceanic waters than the *Crassostrea* type. The clearer oceanic waters are conceded to be less rich in plankton than the estuarine areas, and hence the acceptance of everything small enough would be advantageous. Perhaps this is true. Certainly the *Ostrea* type is adapted to waters of higher salinity, whereas the *Crassostrea* type is predominantly estuarine. However, the importance of nanno-plankton is unknown. It has been found that the *Ostrea* type has larger ostia (correlated with the larviparous condition) than the *Crassostrea* type. Hence the former type would be less efficient in utilizing the very small plankton than the latter. Perhaps utilization of nanno-plankton compensates somewhat for the discrimination in feeding of *Crassostrea* in areas of high salinity or of low turbidity.

Other observations lead to the conclusion that *C. virginica* is better adapted to high turbidity than *O. equestris.* The mantle edges in *C. virginica* usually contract in such a manner that the tentacles intermesh and strain the particles, and allow only the smaller ones to enter the mantle cavity. This behavior was not so common in *O. equestris.* Also *C. virginica* commonly formed pseudosiphons that regulated the intake and exit of water, especially in high turbidity, whereas this was rare in *O. equestris.* The elimination of waste materials was much better in *C. virginica* also. In fact, *O. equestris* caused the pseudofaecal mass to be returned to the palps via the gills unless more particles were entering, and even the faeces were observed to go to the palps and be taken into the stomach.

Summary

A comparison of some phases of the biology of the two genera of oysters, *Ostrea* and *Crassostrea,* represented by *O. equestris* and *C. virginica,* has been presented. In addition, some of the biology of the little-known species *O. equestris* is described, including some features of the life history, anatomy and growth. The detailed studies on the attachment of larval oysters and the feeding habits of the two genera have shown the following differences:

1. *Ostrea (O. equestris)* retains the generic characteristic of spawning at low temperatures, even in warm regions; in warmer regions physiological races of *Crassostrea (C. virginica)* occur which spawn at higher critical temperatures.

2. The spat of *Ostrea* attach subtidally on or near the bottom in waters of high salinity; *Crassostrea* occurs over a wide range of salinities and the spat attach subtidally on or near the bottom in waters of low salinity, but only near the surface or intertidally in high salinity.

3. *Ostrea* is poorly adapted for feeding in waters of high turbidity in the following ways: a). It is selective in feeding only in size of particles. b). There is a poor elimination of waste materials; pseudofaeces and sometimes even the faeces are returned to the palps. c). The mantle seldom contracts to screen out larger particles.

Crassostrea is well adapted for feeding in waters of high turbidity as shown by the following: a). There is selection in feeding that is not related to particle size. b). The elimination of waste materials is very efficient; the pseudofaeces and faeces are never

returned to the palps. c). The mantle usually partially contracts to screen out larger particles, especially in high turbidity.

4. There is an indication that *Ostrea* does not use nanno-plankton extensively for food whereas there is an indication that *Crassostrea* does, even when all larger particles are rejected.

Crassostrea occurs in the unstable estuarine environment where *Ostrea* is not found. Both genera are found in the oceanic environment yet not in the same strata. *Crassostrea* has several physiological and morphological adaptations for feeding in the usually turbid estuarine regions that are not present in *Ostrea.*

BIBLIOGRAPHY

Allen, W. R., 1914. The food and feeding habits of fresh-water mussels. Biol. Bull., 27: 127–139.

———., 1921. Studies on the biology of fresh-water mussels. Experimental studies on the food relation of certain Unionidae. Biol. Bull., 40: 210–241.

Andrews, J. D., 1948. The 1947 oyster strike in the James River. Conven. Natl. Shellfish. Assoc. for 1948: 61–66.

Andrews, J. D., and Willis Hewatt, 1953. Incidence of *Dermocystidium marinum,* Mackin, Owen and Collier. A fungus disease of oysters in Virginia. Conven. Natl. Shellfish. Assoc. for 1953: 79.

Amemiya, I., 1926. Notes on experiments on the early developmental stages of the Portuguese, American and English native oysters, with special reference to the effect of varying salinity. Journ. Mar. Biol. Assoc. U. K., 14: 161–175.

———., 1928. Ecological studies of Japanese oysters, with special reference to the salinity of their habitats. Journ. Coll. Agric., Imp. Univ. Tokyo, 11: 333–381.*

Awati, P. R., and H. S. Rai, 1931. The Bombay Oyster *(Ostrea cucullata).* Indian Zool. Mem., Univ. Lucknow, 3: 1–107.

Baughman, J. L., 1948. An annotated bibliography of oysters, with pertinent material on mussels and other shellfish and an appendix on pollution. Texas A & M Research Found., College Station, Texas, 794 pp.

Baugham, J. L., and B. B. Baker, 1951. Oysters in Texas. Texas Game, Fish and Oyster Comm., Bull. 29: 1–37.

Beaven, G. F., 1949. Growth observations of oysters held on trays at Solomons Island, Maryland. Conven. Natl. Shellfish. Assoc. for 1949: 43–49.

———., 1952. Some observations on rate of growth of oysters in the Maryland area. Conven. Natl. Shellfish. Assoc. for 1952: 90–98.

Binney, W. G., 1858. The complete writings of Thomas Say on the conchology of the United States. Amer. Conch., Part VI: 205–225.

Borradaille, L. A., and F. A. Potts, 1935. The Invertebrata. New York, Macmillan Co. Chap. XVI, The Phylum Mollusca: 543–605.

Brice, J. J., 1896. The fish and fisheries of the coastal waters of Florida. Rep. U. S. Comm. Fish. for 1896: 263–342.

Brooks, W. K., 1880. Observations upon the artificial fertilization of oyster eggs and on embryology of the American Oyster. Ann. Mag. Nat. Hist., 5: 82–83.

———., 1905. The oyster. Baltimore, The Johns Hopkins Press. 1–225.

Bull, H. L., 1927. A note on the chemical composition of "chalky" deposits on the shells of *O. edulis.* Journ. Mar. Biol. Assoc. U. K., 14: 953–954.

Burkenroad, M. D., 1931a. Sex in the Louisiana oyster, *Ostrea virginica.* Science, 74: 71–72.

———., 1931b. Notes on the Louisiana conch, *Thais haemostoma* Linn., in its relation to the oyster, *Ostrea virginica.* Ecol., 12: 656–664.

———., 1953. Two new methods of research on behavior of the oyster. Conven. Natl. Shellfish. Assoc. for 1953: 9–12.

Butler, P. A., 1952a. Shell growth versus meat in the oyster, *C. virginica.* Conven. Natl. Shellfish. Assoc. for 1952: 157–162.

———., 1952b. Seasonal growth of oysters *(C. virginica)* in Florida. Conven. Natl. Shellfish. Assoc. for 1952: 188–191.

———., 1953a. Importance of local environment in oyster growth. Proc. Gulf and Caribb. Fish. Inst., 5: 99–106.

————————., 1953b. The southern oyster drill. Conven. Natl. Shellfish. Assoc. for 1953: 67–75.

————————., 1953c. The oyster predation problem. Southern Fisherman, 13: 35, 58, 88.

Carriker, M. R., 1951a. Ecological observations on the distribution of oyster larvae in New Jersey estuaries. Ecol. Monogr., 21: 19–38.

————————., 1951b. Observations on the penetration of tightly closed bivalves by *Buscyon* and other predators. Ecol., 32: 73–83.

Cary, L. R., 1907. The cultivation of oysters in Louisiana. Bull. Gulf Biol. Stat., 8: 1–56.

Castillo, L., and Z. Vergara, 1907. Apuntes biolojicus e industriales sabre la ostra Chile. Ministero de Industriales, 59 pp.*

Chapman, W. M., and G. D. Esveldt, 1943. The spawning and setting of the Pacific oyster *(Ostrea gigas* Thunberg) in the State of Washington in 1942. Biol. Rept., Dept. of Fish., State of Wash., No. 43A: 1–61.

Chestnut, A. F., 1950. Studies on the digestive system of oysters. Conven. Natl. Shellfish. Assoc. for 1950: 11–15.

Chestnut, A. F., and W. E. Fahy, 1952. Studies on the setting intensity of oysters in Bogue Sound, North Carolina. Conven. Natl. Shellfish. Assoc. for 1952: 78–89.

————————., 1953. Studies on the vertical distribution of setting of oysters in North Carolina. Proc. Gulf and Caribb. Fish. Inst., 5: 106–112.

Churchill, E. P., 1916. The absorption of nutriment in fresh water mussels. Journ. Exper. Zool., 21: 403–424.

————————., 1920. The oyster and oyster industry of the Atlantic and Gulf Coasts. Rept. U. S. Comm. Fish., for 1919, Doc. 890, 1–51.

Churchill, E. P., and S. I. Lewis, 1924. Food and feeding in fresh water mussels. Bull. U. S. Bur. Fish., 39: 437–471.

Coe, W. R., 1931a. Spermatogenesis in the California oyster *(Ostrea lurida).* Biol. Bull., 61: 309–315.

————————., 1931b. Sexual rhythm in the California oyster *(Ostrea lurida).* Science, 74: 247–249.

————————., 1932a. Development of the gonads and the sequence of the sexual phases in the California oyster *(Ostrea lurida).* Bull. Scripps Instit. Oceanogr., Univ. Calif., Ser. 3: 119–144.

————————., 1932b. Sexual phases in the American oyster *(Ostrea virginica).* Biol. Bull., 63: 419–441

————————., 1932c. Season of attachment and rate of growth of sedentary marine organisms at the pier of the Scripps Institution of Oceanography. Scripps Instit. Oceanogr., Univ. Calif., Tech. Ser. 3: 37–86.

————————., 1932d. Historical basis of sex change in the American oyster *(Ostrea virginica).* Science, 76: 125–127.

————————., 1934. Alternation of sexuality in the oviparous oyster, *Ostrea virginica.* Amer. Nat., 68: 236–251.

————————., 1936a. Environment and sex in the oviparous oyster, *Ostrea virginica.* Biol. Bull., 71: 353–359.

————————., 1936b. Protandry in the Virginian oyster. Anat. Rec. (Suppl. I), 67: 89.

————————., 1938. Primary sexual phases in the oviparous oyster *(Ostrea virginica).* Biol. Bull., 74: 64–75.

————————., 1948. Nutritional, environmental conditions and growth of marine bivalve mollusks. Journ. Mar. Resch., 7: 586–601.

Cole, H. H., 1937. Metamorphosis of the larvae of *Ostrea edulis.* Nature, 139: 413–414.

————————., 1938. The fate of the larval organs in the metamorphosis of *Ostrea edulis.* Journ. Mar. Biol. Assoc. U. K., 22: 469–485.

————————., 1942. Primary sex-phases in *Ostrea edulis.* Quart. Journ. Micr. Soc., 83: 317–356.

Cole, H. H., and E. W. Knight-Jones, 1939. Some observations and experiments on the setting behavior of larvae of *Ostrea edulis.* Journ. du Conseil. Exp. Mer., 14: 86–105.*

————————., 1949. The setting behaviour of larvae of the European flat oyster, *O. edulis* L., and its influence on methods of cultivation and spat collection. Fish. Invest., London, Ser. II, 17: 1–39.*

Cooke, A. H. 1895. Molluscs. The Cambridge Natural History. London, Macmillan and Co., Ltd., pp. 244–276.

Dall, W. H., 1898. Contributions to the tertiary fauna of Florida. Trans. Wagner Free Inst. Sci., Phil., 3: 677–688.

Danglade, E., 1919. The flatworm as an enemy of Florida oysters. Rept. U. S. Comm. Fish., 1918, App. V: 1–8.

Dean, B., 1892. The physical and biological characteristics of natural oyster grounds of South Carolina. Bull. U. S. Fish. Comm., 10: 335–362.

de Laubenfels, M. W., 1947. Ecology of the sponges of a brackish water environment at Beaufort, N. C. Ecol. Monog., 17: 31–46.

Elsey, C. R., 1934. Distribution of oyster larvae. Prog. Rept. Pacif. Biol. Stat. and Pac. Exper. Stat. (Canada), 22: 19.*

————., 1935. On the structure and function of the mantle and gills of *Ostrea gigas* (Thunberg) and *Ostrea lurida* (Carpenter). Trans. Roy. Soc. Canada, Sect. 5: 131–160.

Federighi, H., 1929. Temperature characteristics for the frequency of heart beat in *Ostrea virginica* Gmelin. Journ. Exper. Zool., 54: 89–94.

Federighi, H., and A. W. Collier, 1935. Survey of oyster pests of the Texas Coast (Manuscript).*

Fujita, T., 1930. On the early development of the common Japanese oyster. Proc. 4th Pacific Sci. Cong., 3: 357–362.*

————., 1934. Note on the Japanese oyster larvae. Proc. 5th Pacific Sci. Cong., 5: 4111–4117.*

Gaarder, T., and R. Spärck, 1932. Hydrographisch-biochemische Untersuchungen in Norwegischen Austern Pollen. Bergens Museum Årbok, Naturvidenskapelig Rekke, 1932: 1–144.

Galtsoff, P. S., 1926. New methods to measure the rate of flow produced by the gills of oysters and other molluscs. Science, 63: 233–234.

————., 1928a. The effect of temperature on the mechanical activity of the gills of oysters *(Ostrae virginica* Gm.). Journ. Gen. Physiol., 11: 415–431.

————., 1928b. Experimental study of the function of the oyster gills and its bearing on the problems of oyster culture and sanitary control of the oyster industry. Bull. U. S. Bur. Fish., 44: 1–39.

————., 1937. Observations and experiments on sex change in adult American oyster, *Ostrea virginica.* Biol. Bull., 73: 356.

Galtsoff, P. S., H. F. Prytherch, R. O. Smith and V. Koehring, 1935. Effects of crude oil pollution on oysters in Louisiana waters. Bull. U. S. Bur. Fish., 48: 142–210.

Galtsoff, P. S., W. A. Chipman, J. B. Engle and H. N. Calderwood, 1947. Ecological and physiological studies of the effect of pulp mill wastes on oysters in the York River, Virginia. U. S. Fish. Bull., 51: 59–186.

Glaser, O. C., 1905. Observations and experiments on the growth of the oyster. Rept. U. S. Comm. Fish., 29: 329–341.

Grave, C., 1916. The process of feeding in the oyster. Science, 44: 178–181.

Gunter, G., 1950. The generic status of living oysters and the scientific name of the common American species. Amer. Midl. Nat., 43: 438–449.

————., 1951a. The West Indian tree oyster on the Louisiana coast, and notes on growth of three Gulf oysters. Science, 113: 516–517.

————., 1951b. The species of oysters of the Gulf, Caribbean and West Indian region. Bull. Mar. Sci. Gulf Caribb. 1: 40–45.

Gutsell, J. S., 1926. A hermaphroditic viviparous oyster of the Atlantic coast of North America. Science, 64: 450.

Hedgpeth, J. W., 1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. Pub. Instit. Mar. Sci. (Univ. Texas), III (1): 105–224.

Hewatt, W. G., 1952. An oyster feeding experiment. Conven. Natl. Shellfish. Assoc. for 1952: 192–193.

Higgins, E., 1931. Progress in biological inquiries. Doc. 1096, Appen. 15, Rept. U. S. Comm. Fish., 1930: 1069–1121.

Hopkins, A. E., 1931. Temperature and shell movements in oysters. Bull. U. S. Bur. Fish., 47: 1–14.

————., 1933. Experiments on the feeding behavior of the oyster, *Ostrea gigas.* Journ. Exper. Zool., 64: 469–494.

————., 1934a. Accessory hearts in the oyster. Science, 80: 411–412.

————., 1934b. Accessory hearts in the oyster. Biol. Bull., 67: 346–355.

————., 1935a. Attachment of the Olympia oyster, *Ostrea lurida,* to plane surfaces. Ecology, 16: 82–87.

————., 1935b. Temperature optima in the feeding mechanisms of the oyster, *Ostrea gigas.* Journ. Exper. Zool., 71: 195–208.

————., 1936a. Pulsation of blood vessels in oysters, *Ostrea lurida* and *O. gigas.* Biol. Bull. 70: 413–425.

————., 1936b. Ecological observations on spawning and early larval development in the Olympia oyster, *Ostrea lurida.* Ecology, 17: 551–556.

————., 1936c. Activity of the adductor muscle in oysters. Physiol. Zool., 9: 498–507.

————., 1937. Experimental observations on spawning, larval development and setting in the Olympia oyster, *Ostrea lurida.* Bull. U. S. Bur. Fish., 48: 439–503.

Hopkins, S. H., J. G. Mackin and R. W. Menzel, 1953. The annual cycle of reproduction, growth and fattening in Louisiana oysters. Conven. Natl. Shellfish. Assoc. for 1953: 39–42.

Hori, J., 1926. Notes on the full-grown larvae and spat of the Japanese common oyster, *Ostrea gigas* Thunberg. Journ. Imp. Fish. Inst. (Japan), 31: 1–10.*

Ingle, R. M., 1950. Summer growth of the American oyster in Florida waters. Science, 112: 338–339.

Ingle, R. M., and C. E. Dawson, 1952. Growth of the American oyster, *Crassostrea virginica* (Gmelin) in Florida waters. Bull. Mar. Sci. Gulf Caribb., 2: 393–404.

Kellogg, J. L., 1892. A contribution to our knowledge of the morphology of lamellibranchiate molluscs. Bull. U. S. Fish. Comm., 10: 389–436.

————., 1915. Ciliary mechanism of lamellibranchs. Journ. Morph., 26: 625–701.

Knudsen, M., 1946. Hydrographical tables. Reprinted by Woods Hole Oceanographic Institution, Woods Hole, Mass., pp. i–v, 1–63.

Korringa, P., 1941. Experiments and observations on swarming, pelagic life and setting in the European flat oyster, *Ostrea edulis* L. Arch. Neerland. Zool., 5: 1–249.

————., 1952. Recent advances in oyster biology. Quart. Rev. Biol. 27: 266–365.

Landau, H., and P. S. Galtsoff, 1951. Distribution of *Nematopsis* infection in the oyster grounds of the Chesapeake Bay and in other waters of the Atlantic and Gulf States. Texas Journ. Sci., 3: 115–130.

Loosanoff, V. L., 1933. Observations on propagation of oysters in the James and Corrotoman rivers and the Seaside of Virginia. Va. Comm. Fish. (Newport News), 1–46.

————., 1947. Growth of oysters of different ages in Milford Harbor, Connecticut. Conven. Natl. Shellfish. Assoc. for 1946: 12–21.

————., 1949. On the food selectivity of oysters. Science, 110: 122.

————., 1950. Rate of water pumping and shell movement of oysters in relation to temperature. Anat. Rec., 108: Abst. 229.

Loosanoff, V. L., and J. B. Engle, 1940. Spawning and setting of oysters in Long Island in 1937 and a discussion of the method for predicting the intensity and time of oyster setting. Bull. U. S. Bur. Fish., 49: 217–255.

————., 1947a. Effect of different concentrations of micro-organisms on the feeding of oysters *(O. virginica).* Bull. U. S. Bur. Fish., 42: 31–47.

————., 1947b. Feeding of oysters in relation to density of micro-organisms. Science, 105: 260–261.

Loosanoff, V. L., and C. A. Nomejko, 1949. Growth of oysters, *O. virginica,* during different months. Biol. Bull., 97: 82–94.

Loosanoff, V. L., and F. D. Tomers, 1948. Effect of suspended silt and other substances on rate of feeding of oysters. Science, 107: 69–70.

Lotsy, J. D., 1893. The food of the oyster, clam and ribbed mussel. Rept. U. S. Comm. Fish., 19: 375–386.

Lunz, G. R., 1941. *Polydora,* a pest in South Carolina oysters. Journ. Elisha Mitchell Sci. Soc., 57: 273–283.

————., 1947. *Callinectes* versus *Ostrea.* Journ. Elisha Mitchell Sci. Soc., 63: 81.

Mackin, J. G., 1946. A study of oyster strike on the Seaside of Virginia. Contrib. Va. Fish. Lab., No. 25: 1–18.

————., 1951, Histopathology of infection of *Crassostrea virginica* (Gmelin) by *Dermocystidium marinum* Mackin, Owen and Collier. Bull. Mar. Sci. Gulf Caribb., 1: 72–87.

Mackin, J. G., and F. Cauthron, 1952. Effect of heavy infestations of *Polydora websteri* Hartman on *Crassostrea virginica* (Gmelin) in Louisiana. Conven. Natl. Shellfish. Assoc. for 1952: 14–24.

Mackin, J. G., H. M. Owen, and A. Collier, 1950. Preliminary note on the occurrence of a new protistan parasite, *Dermocystidium marinum,* n. sp., in *Crassostrea virginica* (Gmelin). Science 111: 328–329.

Manning, J. H., 1952. Setting of oyster larvae and survival of spat in the St. Mary's River, Maryland, in relation to fouling of cultch. Conven. Natl. Shellfish. Assoc. for 1952: 70–78.

Martin, G. W., 1923. Food of the oyster. Bot. Gaz., 75: 143–169.

————., 1927. Utilization of food by young oysters. Bull. N. J. Exper. Stat., 442: 1–12.

————., 1928. Experimental feeding of oysters. Ecology, 9: 48–55.

Mattox, N. T., 1949. Studies on the biology of the edible oyster, *Ostrea rhizophorae* Guilding in Puerto Rico. Ecol. Monogr., 19: 339–356.

McDougall, K. D., 1943. Sessile marine invertebrates at Beaufort, North Carolina. Ecol. Monogr., 13: 321–374.

McGinitie, G. E., 1941. On method of feeding of four pelecypods. Biol. Bull., 80: 18–25.

Menzel, R. W., 1951. Early sexual development and growth of the American oyster in Louisiana waters. Science, 113: 719–721.

————., 1953. The prodissoconchs and the setting behavior of three species of oysters. Conven. Natl. Shellfish. Assoc. for 1953: 104–112.

Moore, H. F., 1898. Report on the oyster beds of Louisiana. Rept. U. S. Comm. Fish., 24: 45–100.

————., 1905. Anatomy, embryology and growth of the oyster. Rept. U. S. Comm. Fish., 1903: 317–327.

Moore, H. F., and T. E. B. Pope, 1910. Oyster culture experiments and investigations in Louisiana. U. S. Bur. Fish., Doc. 731: 1–52.

Moore, R. C., C. G. Lalicker and A. G. Fischer, 1952. Invertebrate fossils. New York, McGraw-Hill Co., Inc., pp. 400–451.

Morse, D. C., 1944. Some observations on the feeding of oysters in Chesapeake Bay. Conven. Natl. Shellfish. Assoc. for 1944: 17–19.

Needler, A. B., 1932. Sex reversal in *Ostrea virginica*. Contrib. Can. Biol., 7: 285–294.

Needler, A. W. H., 1933. Floats for the collection of oyster spat. Prog. Rept. Atl. Biol. Stat. (Canada), 7: 8–9.*

Nelson, J., 1901. Renewed studies in oyster culture. N. J. Agric. Exper. Stat. for 1900: 315–360.

————., 1902. Report of the Biology Department. N. J. Agric. Exper. Stat. for 1901: 305–381.

————., 1903. Report of the Biology Department. N. J. Agric. Exper. Stat. for 1902: 329–458.

————., 1908. Report of the Biology Department. N. J. Agric. Exper. Stat. for 1907: 205–269.

————., 1914. Report of the Biology Department. N. J. Agric. Exper. Stat. for 1913: 489–534.

Nelson, T. C., 1918. On the origin, nature and function of the crystalline style of lamellibranchs. Journ. Morph., 31: 53–111.

————., 1921a. Aids to successful oyster culture. I. Procuring the seed. N. J. Agric. Exper. Stat., Bull. 351: 1–59.

————., 1921b. Observations on the feeding habits of oysters. Anat. Rec., 20: 181–182.

————., 1922. Report of the Biology Department. N .J. Agric. Exper. Stat. for 1921: 287–299.

————., 1923a. On the feeding habits of oysters. Proc. Soc. Exper. Biol. Med., 21: 90–91.

————., 1923b. The mechanism of feeding of oysters. Proc. Soc. Exper. Biol. Med., 21: 166–168.

————., 1924. The attachment of oyster larvae. Biol. Bull., 46: 143–151.

————., 1925a. Report of the Biology Department. N. J. Agric. Exper. Stat. for 1924: 237–248.

————., 1925b. Recent contributions to the knowledge of the crystalline style of lamellibranchs. Biol. Bull., 49: 86–99.

————., 1926. Report of the Biology Department. N. J. Agric. Exper. Stat. for 1925: 281–288.

————., 1927. Report of the Biology Department. N. J. Agric. Exper. Stat. for 1926: 103–113.

————., 1928. Relation of spawning of oysters to temperature. Ecology, 9: 145–154.

————., 1930. Report of the Biology Department. N. J. Agric. Exper. Stat. for 1929: 95–104.

————., 1933. On the digestion of animal forms by the oyster. Proc. Soc. Exper. Biol. Med., 30: 1287–1290.

————., 1938. The feeding mechanisms of the oyster. I. On the pallium and branchial chambers of *O. virginica, O. edulis* and *O. angulata*. Journ. Morph., 63: 1–61.

————., 1946. Circulation of embryos in the branchial chamber of *O. cristata*. Anat. Rec., 94: 355.

————., 1950. On the function of the mantle, gills and palps of the oyster with special reference to their operation in turbid waters. Conven. Natl. Shellfish. Assoc. for 1950: 1–10.

————., 1952. Some observations on the migration and setting of oysters larvae. Conven. Natl. Shellfish. Assoc. for 1952: 99–104.

Nelson, T. C., and E. B. Perkins, 1931. Report of the Biology Department. N. J. Agric. Exper. Stat. for 1930: 1–47.

Nelson, T. C., and L. A. Stauber, 1940. Observations of some common polychaetes in New Jersey oyster beds, with special reference to *Polydora*. Anat. Rec., 78: 102.

Nelson, T. C., and C. M. Yonge, 1947. On the early development of the gill of the oyster and its bearing upon the phylogeny of ctenidia of Lamellibranchia. Anat. Rec. (Abst. 110), 99: 607.

Newcombe, C. L., and R. W. Menzel, 1945. Future of the Virginia oyster industry. Va. Fish. Lab., Contrib. No. 22: 1–11.

Old, M. C., 1941. The taxonomy and distribution of the boring sponges along the Atlantic Coast of North America. Chesapeake Biol. Lab., Contrib. No. 41: 1–30.

————., 1942. The boring sponges and their effect on shellfish culture. Conven. Natl. Shellfish. Assoc. for 1942: 3 pp.

Orton, J. H., 1912. The mode of feeding of *Crepidula* with an account of the current-producing mechanisms in the mantle cavity, and some remarks on the feeding in gastropods and lamellibranchs. Journ. Mar. Biol. Assoc. U. K., 9: 437–443.

————., 1921. Sex change in the native oyster *(O. edulis). Nature,* 107: 586.

————., 1922. The phenomena and conditions of sex change in oysters *(O. edulis)* and *Crepidula.* Nature, 110: 212–214.

————., 1924. Sex change and breeding in the native oyster, *O. edulis.* Nature 114: 191–192.

————., 1927a. Observations and experiments in sex-change in the European oyster *(O. edulis).* Part I. The change from female to male. Journ. Mar. Biol. Assoc. U. K., 14: 967–1045.

————., 1927b. Researchers in sex-change in the European oyster. Nature 119: 117.

————., 1928. The dominant species of *Ostrea.* Nature, 121: 320–321.

————., 1933. Observations and experiment in sex-change in the European oyster *(O. edulis).* III. On the fate of the unspawned ova. IV. On change from male to female. Journ. Mar. Biol. Assoc. U. K., 19: 1–53.

————., 1935. Biology of shell movements of the oyster. Science, 82: 1–5, 106.

————., 1937. Oyster biology and oyster culture. The Buckland Lectures for 1935, London, Edward Arnold and Co., 1–211.

Orton, J. H. and C. Amigthaligan, 1927. Notes on shell depositions in oysters. Journ. Mar. Biol. Assoc. U. K., 14: 935–953.

————., 1931. Observations and experiments in sex-change in the European oyster *(O. edulis).* Part II. On the gonad of the egg spawning individuals. Journ. Mar. Biol. Assoc. U. K., 17: 315–324.

Owen, H. M., C. R. Maduell, Jr., and R. M. Ingle, Jr., 1949. An ostreodynamometer for studying the activities inside the shell of bivalve mollusks. Science, 109: 148–149.

Owen, H. M., L. L. Walters and L. A. Bregan, 1951. Etiological studies of oyster mortality. I. *Nematopsis ostrearum* Prytherch 1940 (Sporozoa: Porosporidae). Journ. Mar. Resch., 10: 82–90.

Paul, M. D., 1942. Studies on the growth and feeding of certain sedentary organisms in Madras Harbour. Proc. Indian Acad. Sci., B. 15: 1–42.

Parker, T. J., and W. A. Haswell, 1940. A text book of zoology. London, Macmillan and Co., 6th edit., I: 580–609.

Pelseneer, R., 1906. A treatise on zoology (E. R. Lankester, Editor). London, Adam and Charles Black, V: 205–284.

Pearse, A. S., and G. W. Wharton, 1938. The oyster "leech", *Stylochus inimicus* Palombi, associated with oysters on the coast of Florida. Ecol. Monogr., 8: 605–655.

Pomeroy, L., 1952. Radioisotope studies of the utilization of dissolved phosphorus and calcium by the American oyster. Conven. Natl. Shellfish. Assoc. for 1952: 167–180.

Prytherch, H. F., 1929. Investigations of physical conditions controlling spawning of oysters and the occurrence, distribution and setting of oyster larvae in Milford Harbor, Connecticut. Bull. U. S. Bur. Fish., 44: 429–503.

————., 1934. The role of copper in the setting, metamorphosis and distribution of the American oyster, *Ostrea virginica.* Ecol. Monogr., 4: 47–107.

————., 1938. Life cycle of a sporozoan parasite of the oyster. Science, 88: 451–452.

————., 1940. The life cycle and morphology of *Nematopis ostrearum,* sp. nov., a gregarine parasite of the mud crab and oyster. Journ. Morph., 66: 39–65.

Quayle, D. B., 1941. The edible mollusks of British Columbia. Rept. Comm. Fish., Brit. Col., 1940: 675–687.*

Ranson, G., 1936. Sur quelques maladies des huîtres. Rev. Pathologie Comparée, No. 475: 506–526.

—————., 1939. Le provinculum de la prodissoconque de quelques Ostrèides. Bull. Mus. d'Hist. Nat., Paris, 11: 318–331.

—————., 1943. La vie des huîtres. Paris, Gallimard., 3rd Edit., 260 pp.

—————., 1948. Prodissoconques et classification des Ostrèides vivants. Bull. Mus. Roy. d'Hist. Nat. de Belgique, 24: 1–12.

Ray, S. M., 1952a. A culture technique for the diagnosis of infection with *Dermocystidium marinum* Mackin, Owen and Collier in oysters. Science, 116: 360.

—————., 1952b. A culture technique for the diagnosis of infection with *Dermocystidium marinum* in oysters. Conven. Natl. Shellfish. Assoc. for 1952: 9–13.

—————., 1953. Studies on the occurrence of *Dermocystidium marinum* in young oysters. Conven. Natl. Shellfish. Assoc. for 1953: 80–92.

Ray, S. M., J. G. Mackin and J. L. Boswell, 1953. Quantitative measurements of the effect on oysters of disease caused by *Dermocystidium marinum.* Bull. Mar. Sci. Gulf Caribb., 3: 6–24.

Roughley, T. C., 1933. The life history of the Australian oyster, *Ostrea commercialis.* Proc. Linn. Soc. N. S. W., 58: 279–333.

Ryder, J., 1883. On the mode of fixation of the fry of the oyster. Bull. U. S. Fish. Comm., 3: 383–387.

—————., 1884. On the metamorphosis and post larval stages of development of the oyster. Rept. U. S. Fish. Comm. (1882), 10: 779–791.

—————., 1885. The rate of growth of oysters at St. Jerome's Creek Station. Bull. U. S. Fish. Comm., 5: 129–131.

Sandoz, M., and S. H. Hopkins, 1947. Early life history of the oyster crab, *Pinnotheres ostreum* (Say). Biol. Bull., 93: 250–258.

Savage, R. E., 1925. The food of the oyster. Brit. Ministry Agric. Fish., Fish. Invest., Ser. II, 8: 1–50.*

Seki, H., and K. Tanaka, 1931. On collecting spats of *Ostrea denselamellosa.* Imp. Fish. Exper. Stat. (Tokyo), II: 219–230.*

Schiedt, R. C., 1904. Some phenomena of animal pigmentation. Am. Journ. Physiol., 10: 365–372.

Schrock, R. R., and W. H. Twenhofel, 1953. Principles of Invertebrate Paleontology. New York, McGraw-Hill Co., Inc., 2nd Edit., pp. 350–402.

Snedecor, C. W., 1946. Statistical methods. Ames, Iowa State College Press, 4th Edit., 485 pp.

Sprague, V., 1949. Species of *Nematopsis* in *Ostrea virginica.* Journ. Parasit., 35: 42.

Sprague, V., and P. E. Orr, 1952. Studies on *Nematopsis.* III. *N. ostrearum* and *N. prytherchi,* with special reference to host-parasite relation. Conven. Natl. Shellfish. Assoc. for 1952: 26–43.

Stafford, J., 1905. On larva and spat of the Canadian oyster. Amer. Nat., 39: 41–44.

—————., 1909. The larva and spat of the Canadian oyster. I. The larva. Amer. Nat., 43: 31–47.

—————., 1910. The larva and spat of the Canadian oyster. II. The spat. Amer. Nat., 44: 343–366.

—————., 1913. The Canadian oyster, its development, environment and culture. Comm. Conser., Canada, 199 pp.

—————., 1914. The native oyster of British Columbia (*Ostrea lurida* Carpenter). Proc. Brit. Columbia, Rept. Comm. Fish., 1913: 79–102.*

Stauber, L. A., 1945. *Pinnotheres ostreum,* parasite in the American oyster, *Ostrea (Gryphaea) virginica.* Biol. Bull., 88: 269–291.

Takatsuki, S., 1927. Physiological studies of the rhythmical heart pulsations in the oyster, *Ostrea circumpicta* Pils. Tohuku Imp. Univ. Biol., 2: 301–324.*

—————., 1929. The heart pulsations of oysters in tropical seas compared with those living in seas of temperate zone. Rec. Oceanogr. Works Japan, 1: 102–112.*

—————., 1932. Contribution to the physiology of the heart of the oyster. III. An automaticity in the ventricle and auricle of the heart as affected by temperature. Sci. Rept. Tohuku Imp. Univ., 7: 145–156.*

Thomson, J. M., 1954. The genera of oysters and the Australian species. Australian Journ. Mar. and Freshwater Research, 5: 132–168.

Topsent, E., 1887. Contribution a l'étude des Clionides. Arch. Zool. Exper. Gen., Ser. 2, V: 1–165.

—————., 1900. Etude monographique des Spongiarires de France. III. Monaxonida (Hudromerina). Arch. Zool. Exper. Gen., Ser. 3, VIII: 1–331.*

Wakiya, V., 1929. Japanese food oysters. Jap. Journ. Zool. Trans., 2: 359–367.*

Yonge, C. M., 1926. Structure and physiology of the organs of feeding and digestion in ***Ostrea edulis***. Journ. Mar. Biol. Assoc. U. K., 15: 295–386.

ZoBell, C. E., 1938. The sequence of events in the fouling of submerged surfaces. Contrib. Scripps Instit. Oceanogr., N. S. No. 35.*

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* Original publication not seen.

PLATE III

FIG. 9. Graph showing percentages of *O. equestris* and of *C. virginica* that attached at each level in Series A at Port Aransas.

FIG. 10. Graph showing percentages of *O. equestris* and of *C. virginica* that attached at each level in Series B at Port Aransas.

FIG. 11. Graph showing percentages of *O. equestris, O. frons* and *C. virginica* that attached at each level at Pensacola.

PLATE IV

FIG. 12. Camera lucida drawing of *O. equestris* (0.8 mm. length; 0.8 mm. height). A, Region where incurrent pseudosiphon forms; B, region where excurrent pseudosiphon forms; C, pseudofaeces exit; D, point of pseudofaeces tract where pseudofaeces returned to gills; *ad. mu.*, adductor muscle; *an.*, anus; *au.*, auricles; *di. gl.*, digestive gland; *in.*, intestine; *le. gi.*, left gill (lamella) ; *ma.*, mantle; *oe.*, oesophagus; *pa.*, palps; *pr. sh.*, prodissoconch shell; *ps. tr.*, pseudofaeces tract; *sh.*, shell; *st.*, stomach; *st. sa.*, style sac; *ve.*, ventricle.

FIG. 13. Camera lucida drawing of *C. virginica* (1.8 mm. length; 1.9 mm. height). E, region where posterior excurrent pseudosiphon forms; F, "chalky" streak in right valve; G, chalky calcification in left valve; *gi.*, gills; other labels as in Figure 12.

The arrows in both figures indicate the direction and intensity of the currents within the mantle cavity. These arrows represent composite observations.

PLATE V

FIG. 14. Camera lucida drawing of a frontal section of *O. equestris. em.*, embryos; *gi, gills; i. pa.*, inner palps; *ma.*, mantle; *o. pa.*, outer palp; *ps. tr.*, pseudofaeces tract in right mantle.

FIG. 15. Diagram of pseudofaeces tract in *O. equestris. gi.*, gills; *pa.*, palps; *ps. tr.*, pseudofaeces tract; *D*, point of pseudofaeces tract where pseudofaeces returned to gills.

FIG. 16. Diagram of pseudofaeces tract of *C. virginica.* Labels as in Figure 15.

FIG. 17. Semi-diagrammatic camera lucida drawing of palps of *C. virginica.* Arrows indicate currents as seen under 100X magnification.

FIG. 18. Semi-diagrammatic camera lucida drawing of palps of *O. equestris.* Arrows indicate currents as seen under 100X magnification.

FIG. 19. Tip of rectum of *O. equestris,* open and showing cilia.

FIG. 20. Tip of rectum of *O. equestris,* with anus closed.

(Scale A for Figure 14; Scale B for Figures 15, 16, 17, 18, 19, 20 and 21.)

PLATE VI

FIG. 21. Camera lucida drawing of relaxed adductor muscle *(O. equestris).*

FIG. 22. Camera lucida drawing of contracted adductor muscle *(O. equestris).*

FIG. 23. Camera lucida drawing of *O. equestris* showing the hermaphroditic condition. *ov.*, ovum; *sp. ba.*, sperm ball.

FIG. 24. Camera lucida drawing of sperm ball of *O. equestris.*

PLATE VII

FIG. 25. Camera lucida drawing of accessory heart and adjacent structures of *O. equestris. ac. he.*, accessory heart; *an.*, anus; *au.*, auricle; *ad. mu.*, adductor muscle; *ci.*, cilia on tip of rectum; *ci. pa.*, circumpallial blood vessel; *fr. gi.*, blood vessel from gills; *fr. ma.*, blood vessel from mantle; *or. Bo.*, organ of Bojanus; *ve.*, ventricle; *vi. ma.*, visceral mass.

PLATE III

FIG. 9

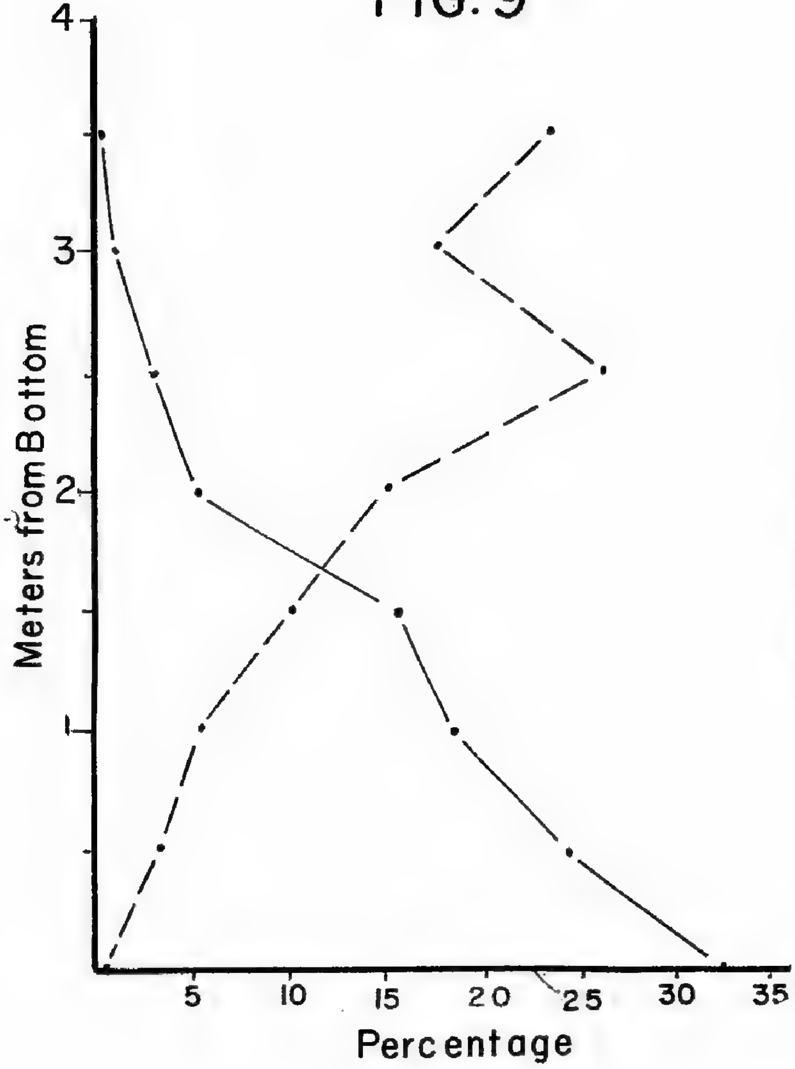
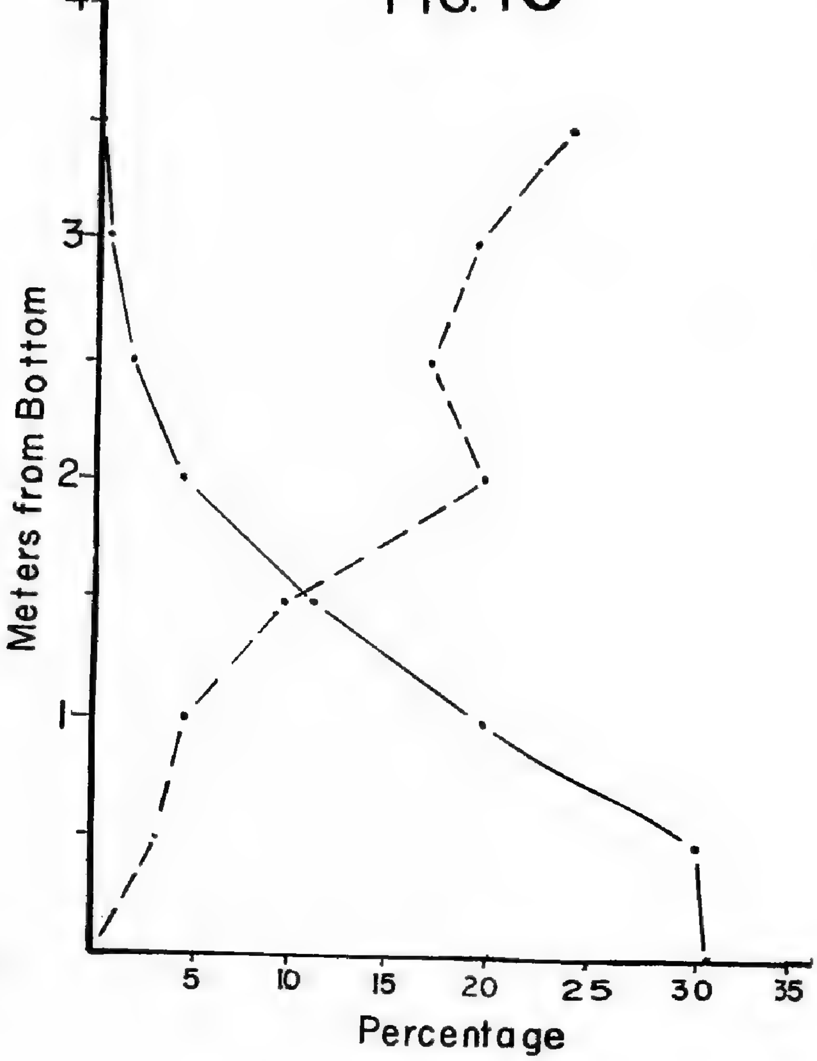


FIG. 10



•——• O. equestris
•— —• C. virginica
×——× O. frons

FIG. 11

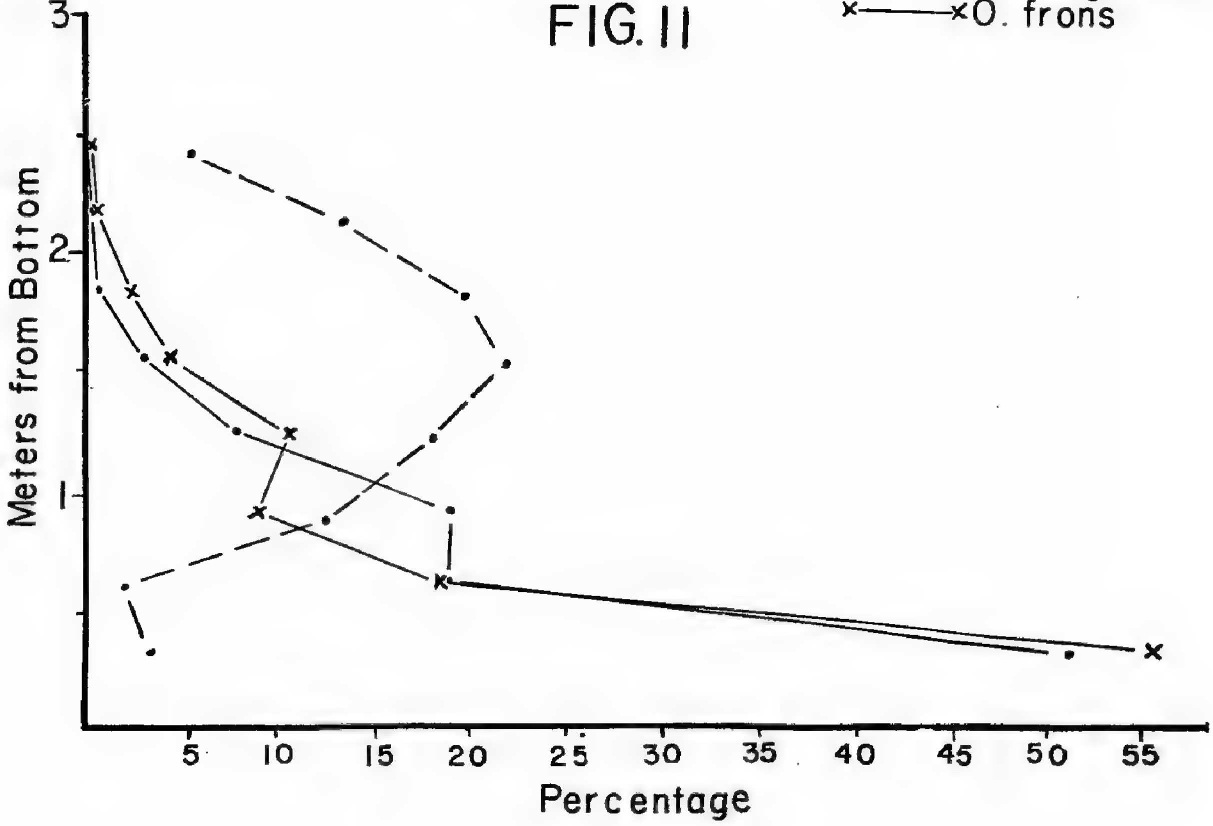
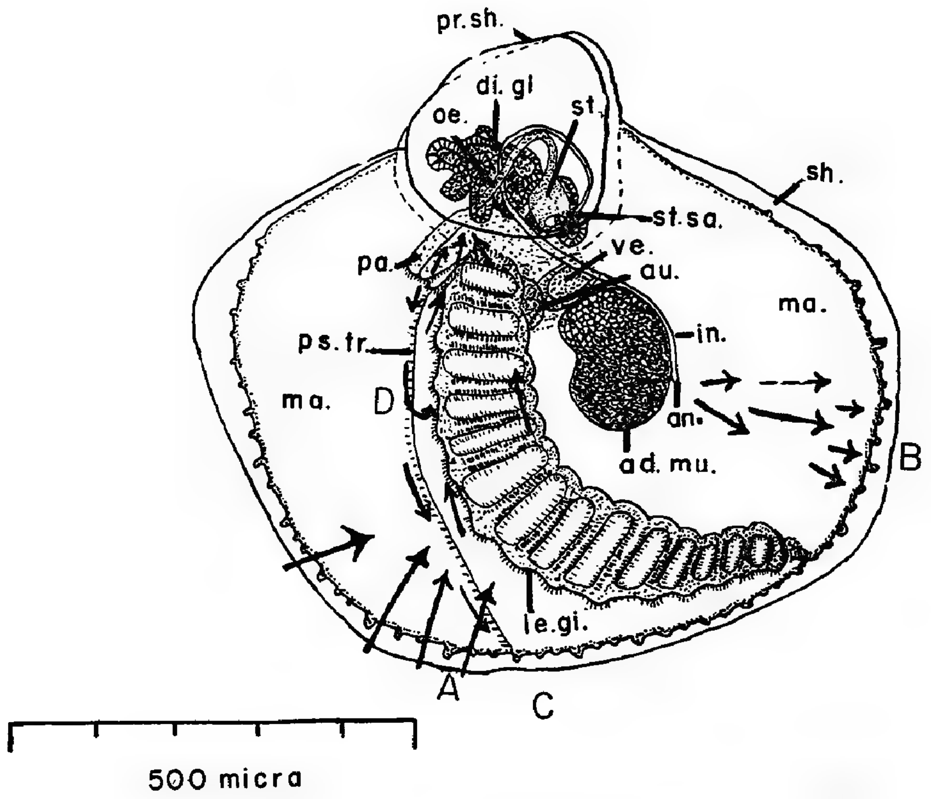


PLATE IV

FIG. 12


pr.sh.
di. gl
oe.
st.
sh.
st.sa.
ve.
au.
pa.
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D
an.
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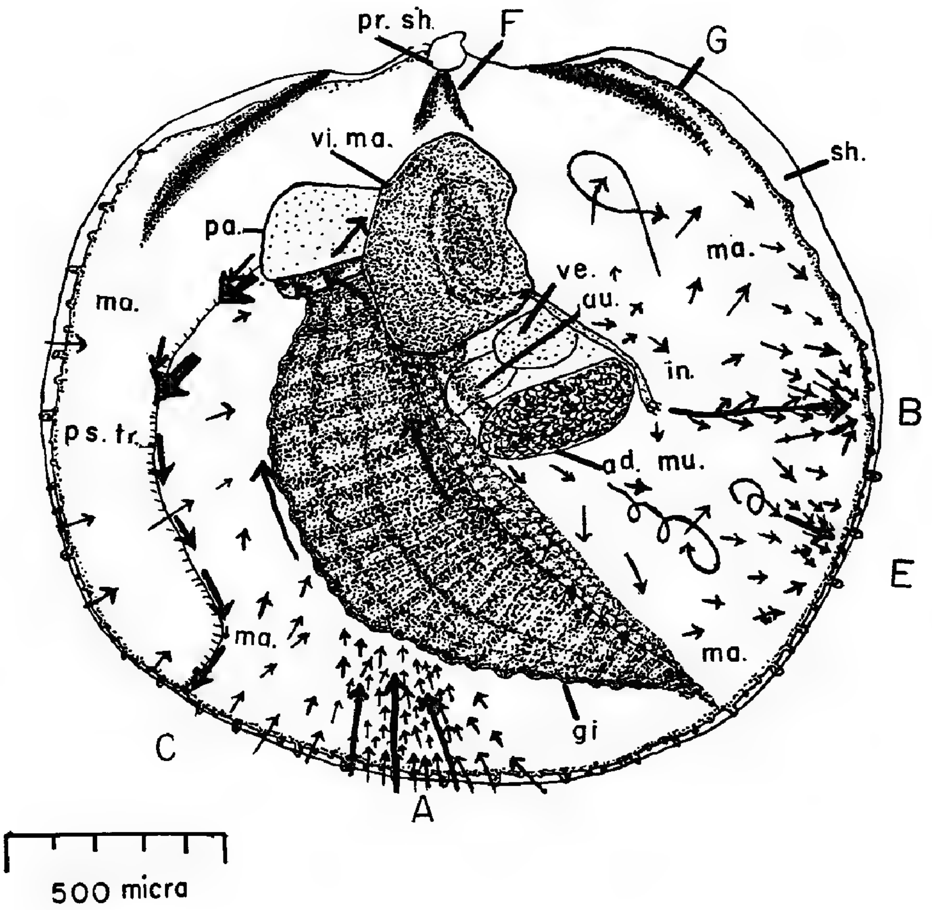
ad. mu.
le.gi.
A
C
500 micra

FIG. 13


pr. sh.
F
G
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vi. ma.
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E
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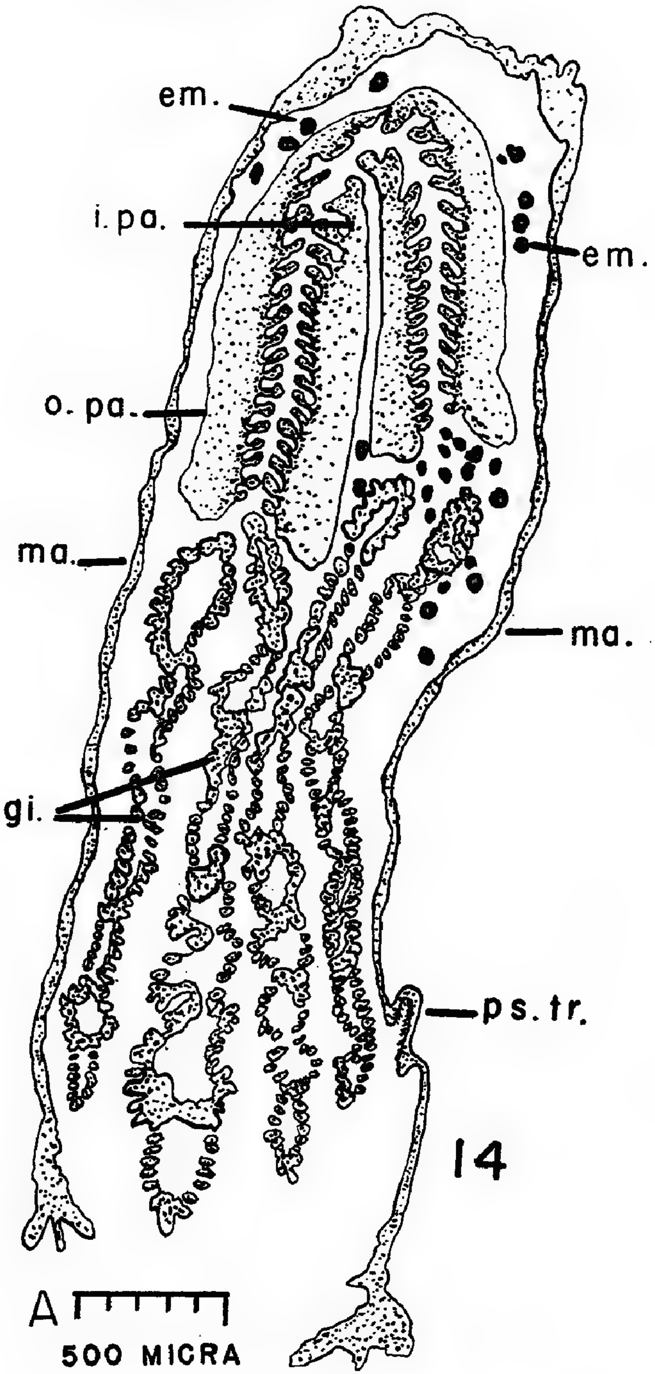
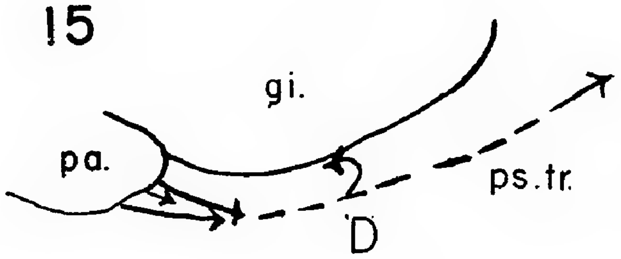
ma.
gi
C
A
500 micra

PLATE V


em.
i. pa.
em.
o. pa.
ma.
ma.
gi.
ps. tr.
A
500 MICRA

14

15



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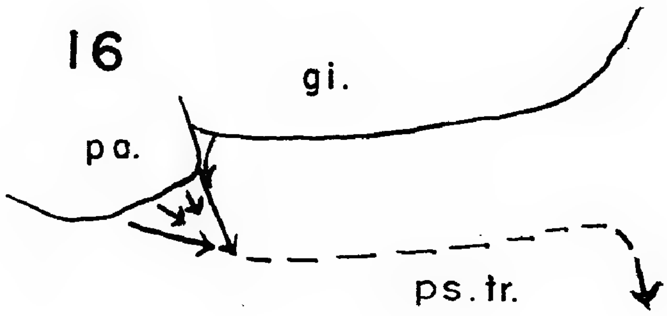

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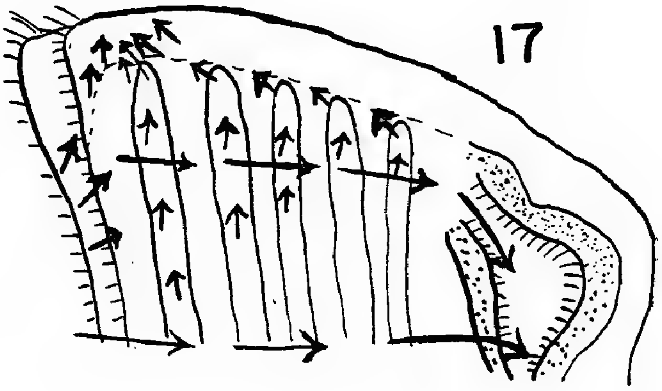

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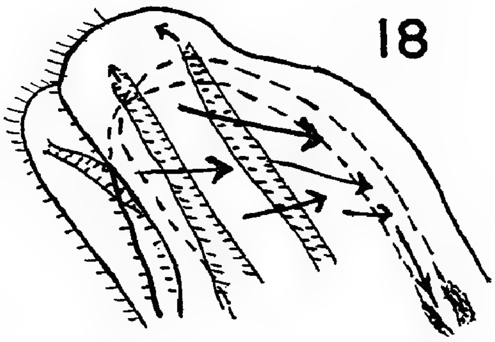

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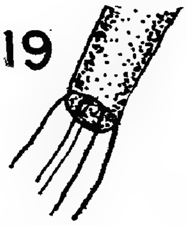
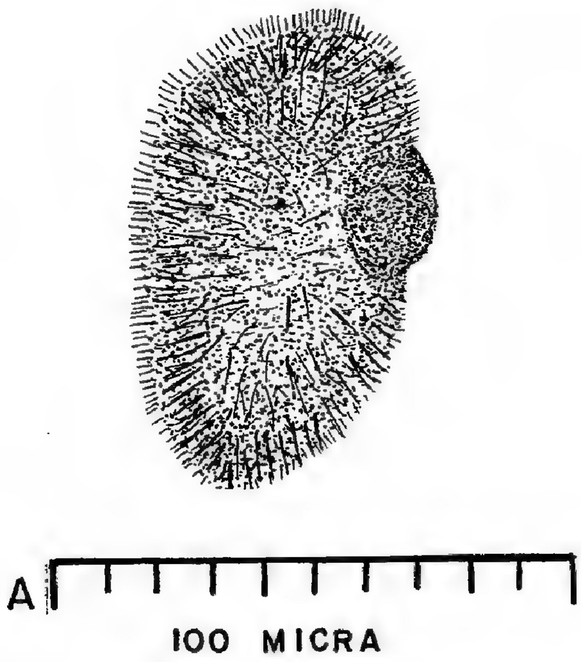


20

PLATE VI

21



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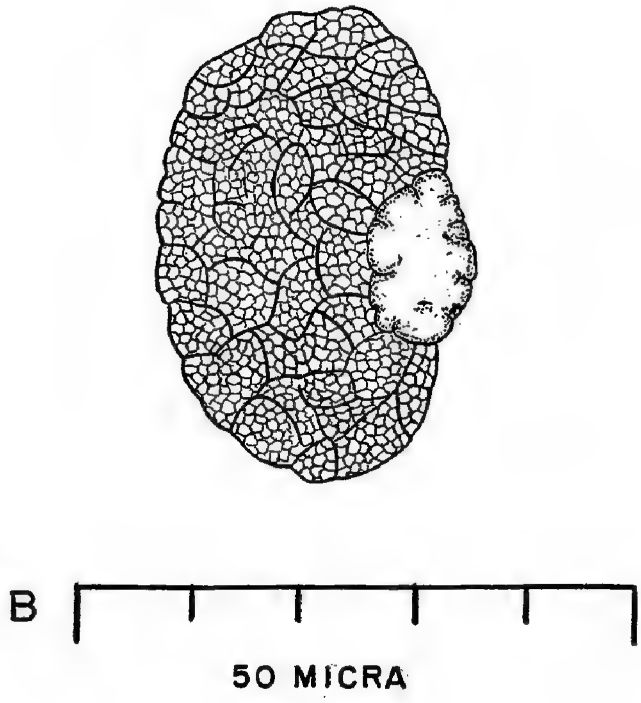

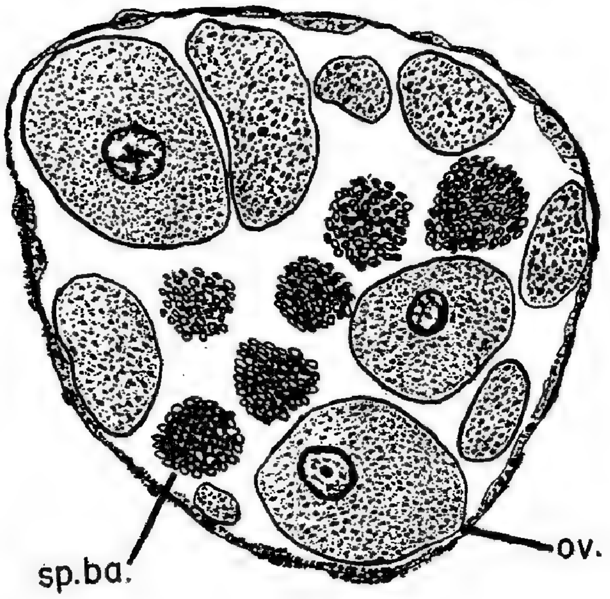

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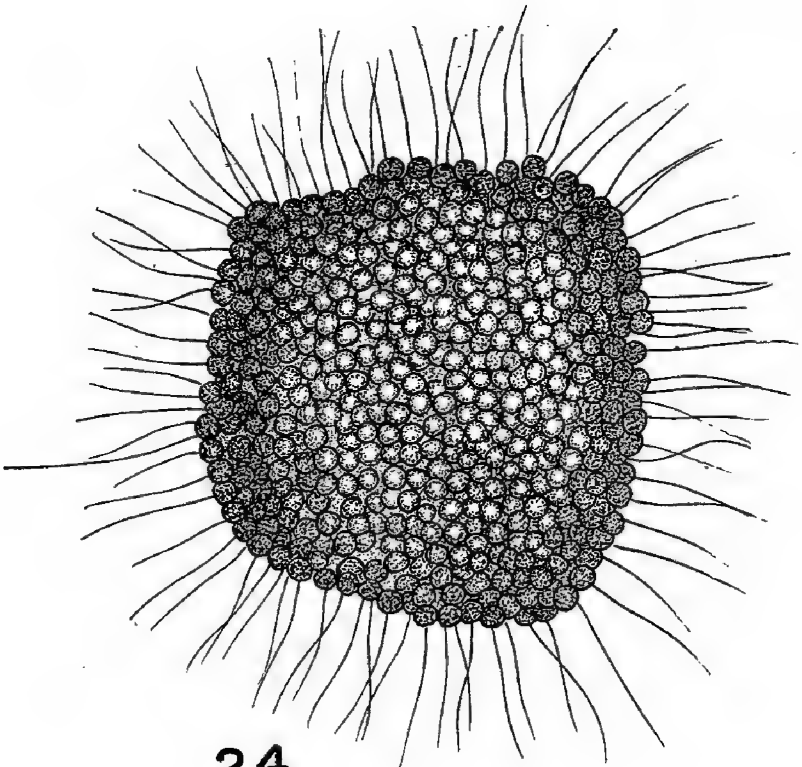
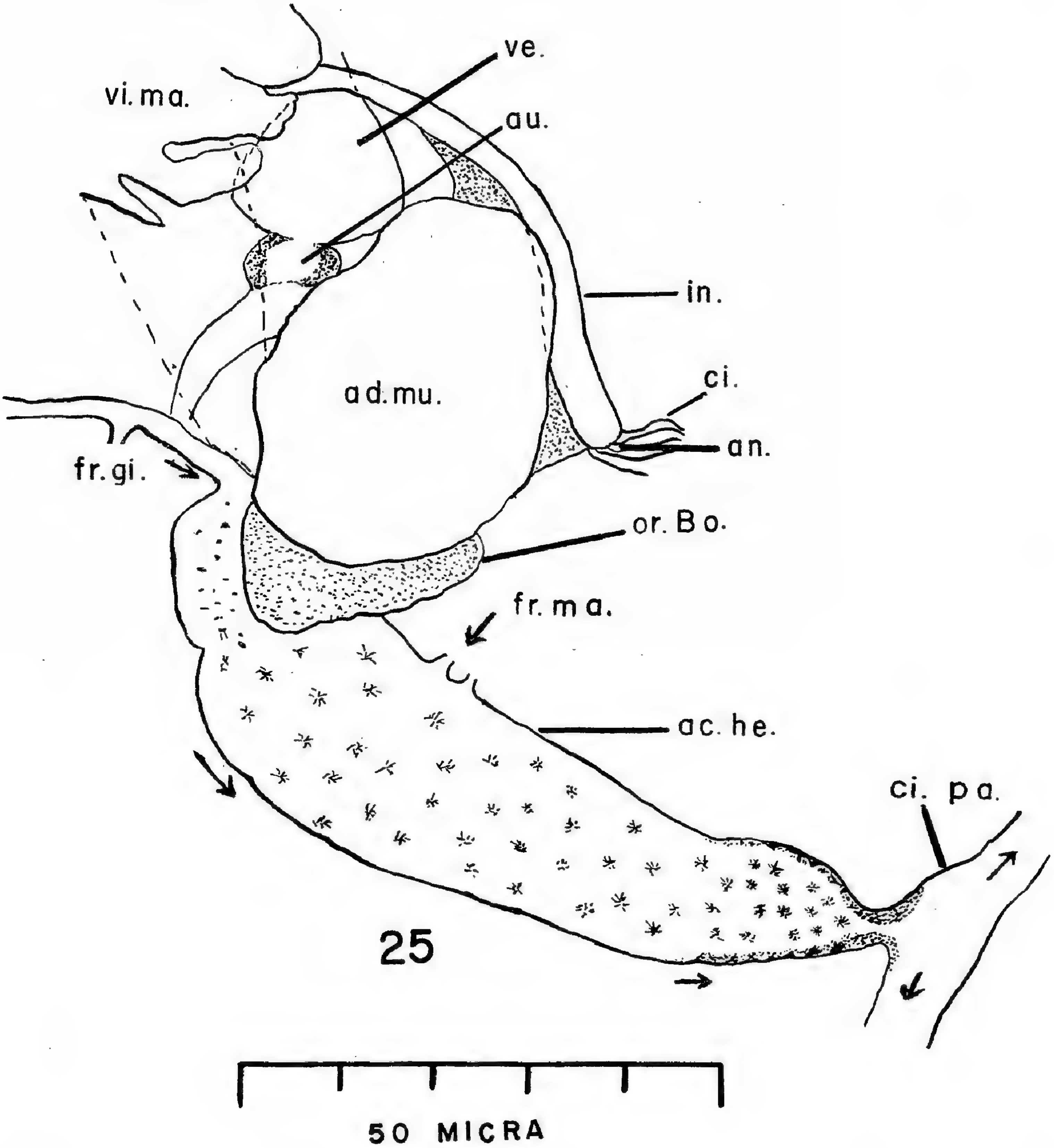


24

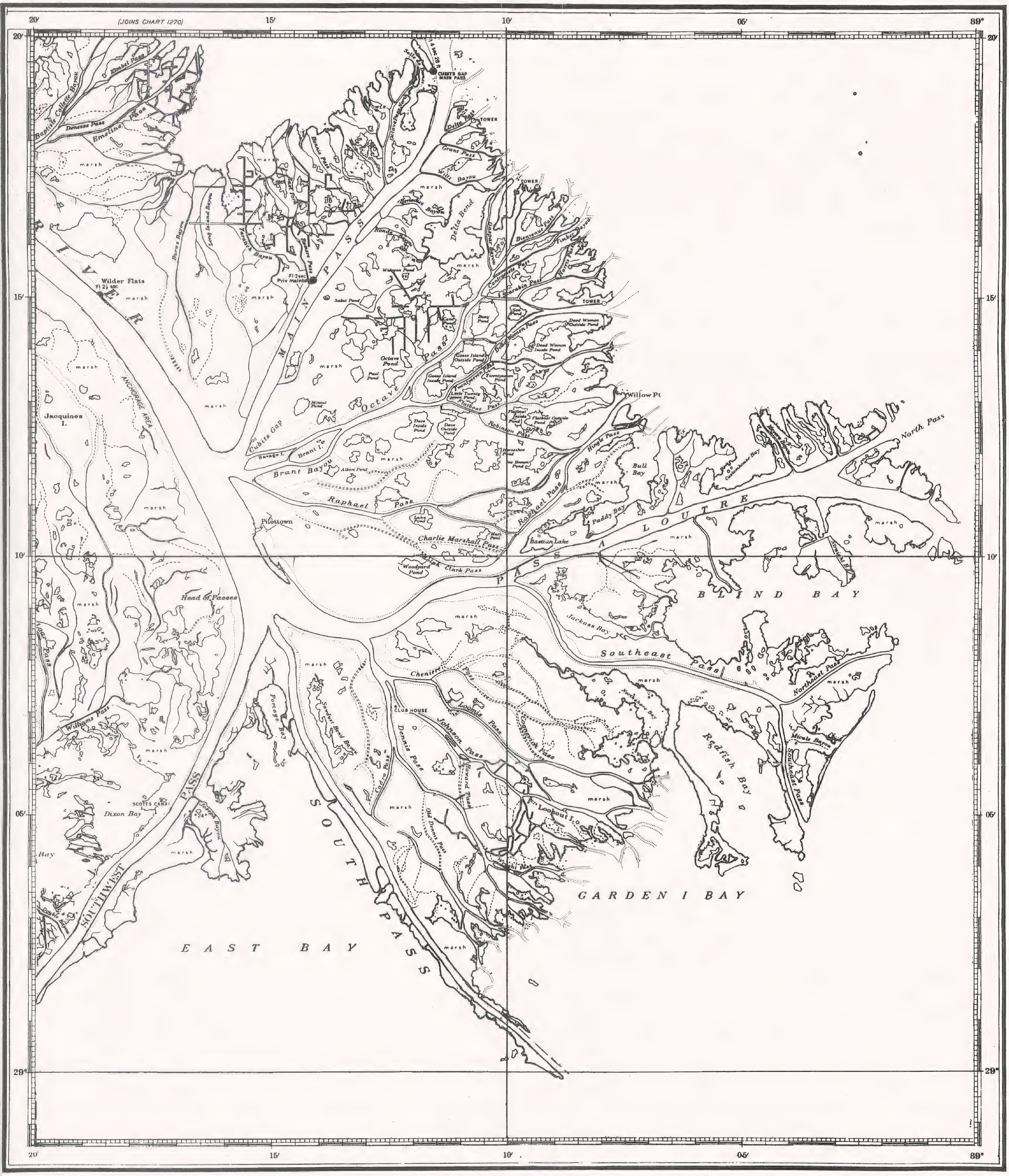
PLATE VII


ve.
vi. ma.
au.
in.
ad. mu.
ci.
an.
fr. gi.
or. Bo.
fr. ma.
ac. he.
ci. pa.
25
50 MICRA

Effect of the Gulf of Mexico and the Mississippi River on Hydrography of Redfish Bay and Blind Bay

By
RICHARD A. GEYER

Humble Oil & Refining Company, Houston, Texas
Present Address, *Geophysical Service, Inc., Houston, Texas*


(JOINS CHART 1270)
20′
15′
10′
05′
89°
29°
Baptiste Collette Bayou
Denesse Pass
Emeline Pass
Kimbel Pass
MAIN PASS
CUBITS GAP MAIN PASS
Delta Bend
Grant Pass
Willis Bayou
TOWER
Bienvenue Pass
Timber Bayou
Long Island Bayou
Buras Bayou
Wilder Flats
Fl 2½ sec
Fl 2 sec Priv maintd
Sabot Pond
Widgeon Pond
Octave Pond
Octave Pass
Paul Pond
Minout Pond
Goose Island Outside Pond
Goose Island Inside Pond
Twentyseven Pond
Little Twenty seven Pond
Flatboat Pass
Dead Women Pass
Dead Woman Outside Pond
Dead Woman Inside Pond
Willow Pt
Robinson Pass
Horseshoe Pond
Flatboat Inside Pond
Flatboat Outside Pond
Cubits Gap
Savage I.
Brant I.
Brant Bayou
Albert Pond
Dave Inside Pond
Dave Outside Pond
Raphael Pass
Lake Pond
Charlie Marshall Pass
Joseph Clark Pass
Woodyard Pond
Pilottown
Bastian Lake
Paddy Bay
Bull Bay
Hingle Pass
PASS A LOUTRE
North Pass
Cadenhouse Bay
BLIND BAY
Jackass Bay
Southeast Pass
Northeast Pass
Redfish Bay
Southeast Pass
Micale Bayou
RIVER
ANCHORAGE AREA
Jacquines I.
Head of Passes
marsh
Cheniere Pass
Loomis Pass
Johnson Pass
Dennis Pass
Sawdust Bend Bayou
Codro Pass
CLUB HOUSE
Howard Pass
Old Dennis Pass
Lookout I.
GARDEN I BAY
Portage Bay
SOUTH PASS
EAST BAY
SOUTHWEST PASS
Williams Pass
Dixon Bay
SCOTTS CANAL
Bay

INDEX MAP OF SURVEY AREA

FIGURE - I

ABSTRACT

A hydrographic survey was conducted in Redfish and Blind Bays, on the southern edge of the Mississippi Delta, and in the adjoining areas in the Gulf of Mexico. Almost 1,100 observations were made at 49 locations during an 8-week period in the spring of 1953. Information was obtained on salinity, temperature, and current conditions.

These data are summarized and evaluated with emphasis on the effect of the Mississippi River and the Gulf of Mexico on the hydrography of Redfish and Blind Bays. A correlation exists between the stage of the Mississippi River and the salinity and temperature characteristics of these bays and their adjoining Gulf areas. Similarly, the diluting effect during high stages of the Mississippi River is evident over an area extending for several miles into the Gulf. It was noted that islands in Redfish Bay are wasting away.

INTRODUCTION

Redfish and Blind Bays lie on the extreme southeastern portion of the Mississippi Delta (Figure 1). The bays are open at one end to the Gulf of Mexico and have connections with the Mississippi River by its distributaries. The waters of Southeast Pass flowing past Redfish Bay on the east, and separated from it by a narrow natural levee, can enter by at least three channels. In addition, during flood stages, the waters from this distributary frequently flow over the natural levee and flood the entire bay area. Blind Bay is connected to Pass à la Loutre by a similar number of channels, and is also inundated during flood stages of the Mississippi.

Redfish Bay covers about 5 square miles and varies in depth from several inches to a maximum of about 5 feet. Blind Bay has an area of about 12 square miles and ranges in depth from a few inches to about 10 feet. These depths apply to normal low tide conditions, but they vary considerably depending upon whether astronomic or wind tides prevail at the moment, and their depth is increased a little with high stages of the Mississippi. Therefore, the hydrographic characteristics of the two bays at any given period are similarly related to the prevailing oceanographic, meteorologic, and river stage conditions.

Early in 1952, drilling operations were scheduled in Redfish Bay by the Humble Oil & Refining Company. It was necessary to cut a canal through the west bank of Southeast Pass to gain access to these locations. Before this action was taken, a study of the existing conditions of Redfish Bay was made to determine what effect additional river water might have on the hydrography of the area.

Before the Humble canal was cut in the summer of 1952, a survey was conducted under the direction of Dr. Gordon Gunter, of the Institute of Marine Science of The University of Texas. The results of this survey showed that even during periods of low stages of the Mississippi, when the saline waters of the Gulf of Mexico dominated the hydrography of the area, the salinity of Redfish Bay could be very low. For example, the salinity at the bottom during one survey averaged about 3.6 parts per thousand. However, the seasonal variations of the hydrographic characteristics of this area made it necessary to conduct similar surveys during other times of the year. The most extensive of these surveys was conducted after the Humble canal was cut during the spring of 1953, and coincided with the period when the river was at its highest stage for that year. More than a thousand hydrographic observations were made at 49 locations during a period between May 5 and July 2. Three observation stations are located in Redfish Bay and 10 in Blind Bay. Thirty-one stations (designated by the letter "G") are located in the Gulf of Mexico in a zone about 2 miles wide and 12 miles long. This zone parallels the shore line and extends from the mouth of Redfish Bay northeastward to the mouth of Blind Bay. The remaining five stations are located in two small unnamed bays opening on to the Gulf, situated between Redfish and Blind Bays. Observations were made of the water temperature, and salinity, both at the surface and on the bottom. In addition, the direction and velocity of the currents were observed at six key points in the area (Figure 5). The results are summarized in a series of charts appearing as Figures 2–8.

SURVEY METHODS

The salinity values obtained during the survey are based primarily on hydrometer readings corrected for water temperature, although several samples were analyzed using conventional titration methods. Current velocity and direction were measured by the method recommended by the United States Coast and Geodetic Survey (USCGS, 1950).

The locations of the 49 stations were established by conventional survey methods and were marked by flagged stakes. Measurements were made at eash of the stations at frequent intervals during the two month's period. These intervals varied from almost daily in the Redfish Bay and adjacent Gulf areas to three times a week in the northern portion of the open Gulf areas, and for the first month in Blind Bay. Observations were discontinued during the second month of the survey in Blind Bay, because an analysis of salinity and temperature data obtained during the first month demonstrated that the hydrographic conditions in this area were very uniform and showed only minor fluctuations. This permitted the major effort of the survey to be placed on a more detailed study of Redfish Bay and adjacent Gulf areas.

HYDROGRAPHIC CHARACTERISTICS OF REDFISH BAY AND BLIND BAY

Topography and Drainage

The United States Coast and Geodetic survey conducted a detailed submarine topographic survey of the area in 1939 (USCGS, 1939). Marshy areas surround Redfish and Blind Bays, and the entire region is inundated during periods of extreme high water when the distributaries of the Mississippi flood their banks. The deepest portion of Redfish Bay is at the upper end where values of three to four feet predominate. The southern portion of the bay varies in depth from one to three feet, with a shallow area one foot or less in depth, roughly paralleling the eastern shore line. The bottom sediments consist for the most part of soft gray mud with occasional patches of hard mud.

Blind Bay varies in depth from a few inches, in the tidal flat areas around the mouth of the Bay and extending into the Gulf, to as much as 7–10 feet in one, small, isolated locality near the center of the Bay. However, the average depth is about 3–4 feet, the same as Redfish Bay. The bottom sediment characteristics compare very closely to those of Redfish Bay.

Several small islands occurred in the central portion of Redfish Bay as shown by the U. S. C. G. S. map based on the 1939 survey. However, this area, in general, has been subsiding during the past 15 to 20 years, and the processes of erosion have dominated over those of deposition. Doctor Gunter pointed out in the typed report of his survey in the spring of 1953, that islands in the bay are wasting away. This is easy to see from an examination of the area and a comparison with the 1939 map. The two small islands shown on the map in the northern part of the bay now consists of a strip of grass 10 to 15 yards long and a yard wide. This observation is of considerable interest geologically. Russell (1936) has shown that large areas east of the lower river have wasted away when they were cut off from sedimentation by artificial levees and he has termed the process "abandonment of alluviation" (Russell, 1948). Gunter (1952) briefly reviewed the information and added a little more for the west side of the river. In these discussions it was assumed or implied that wasting and destruction takes place in areas artificially cut off from river sediments by man-made levees. However, the above observation on Redfish Bay indicates that wasting of land areas also takes place along the lower river in areas far below the artificial levees, and under the full impact of alluviation. In fact, if the upriver artificial levees have any effect in the Redfish Bay area, the most reasonable assumption is that they would increase deposition by funneling all sediments down to the various river mouths.

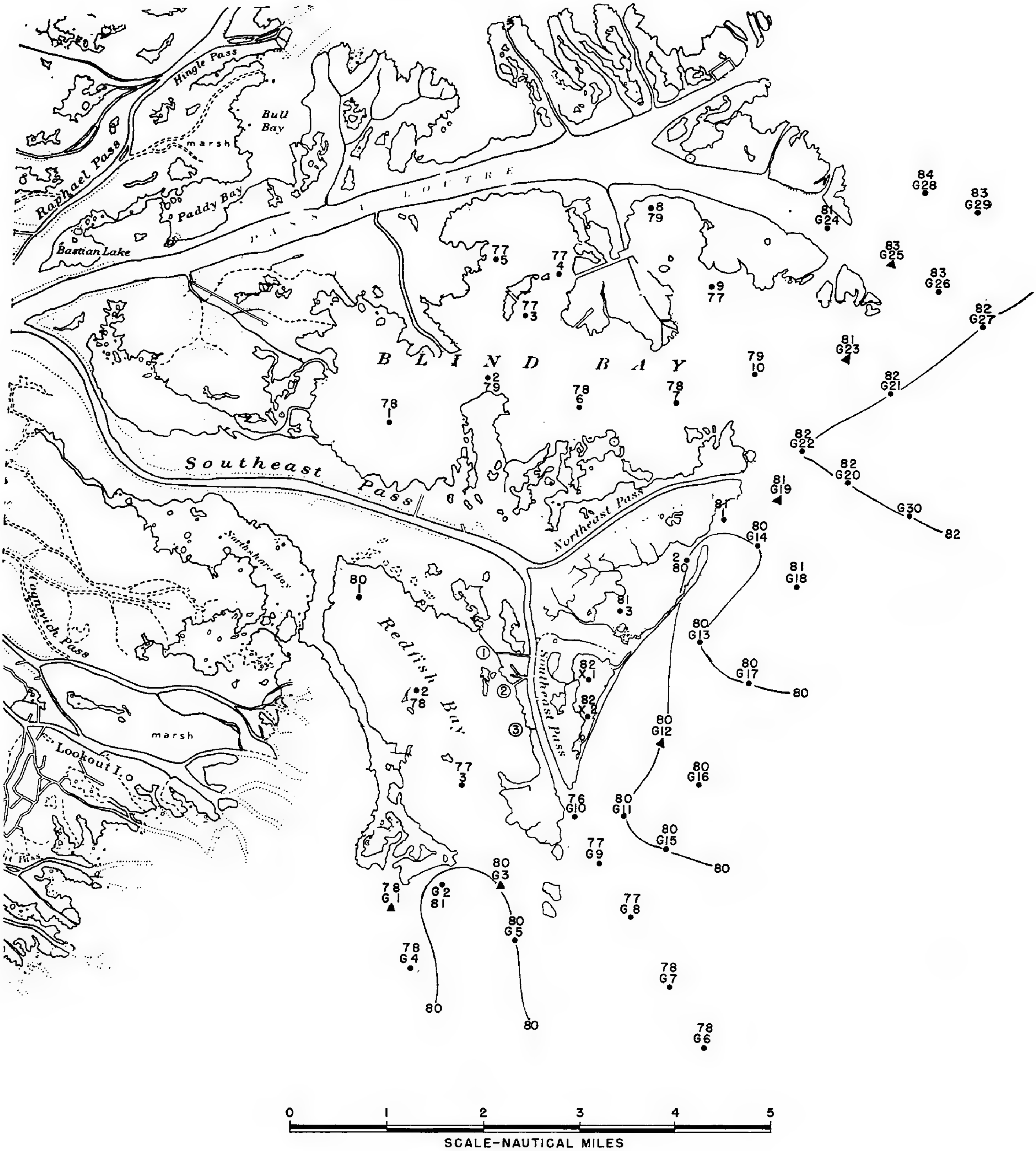
Temperature

During the period, May 5 to June 3, when the stage of the river was still high and a large amount of river water was being discharged through Southeast Pass, sufficient water was flowing to lower the temperature of the water for several miles into the Gulf by as much as three degrees (Figure 2). (A similar situation prevailed at the easternmost mouth of Southeast Pass.) During this period, the average temperatures for Redfish Bay and Blind Bay were 78.3° and 77.9° F, as compared with open Gulf temperatures of 80°–81° F.

On the other hand, during the period, June 4 to July 2, when the river stage was no longer high, the wedges of cold water extending to the Gulf had disappeared. The average temperatures in the bay and contiguous areas in the Gulf ranged between 85 and 86 degrees, and differed by only one degree (Figure 3).

The marked increase of about five degrees or more in the average water temperature is caused by the shallow depth of the bays and the prevailing higher air temperatures during the period, June 4 to July 2, as compared with May 5 to June 3. The combination of prolonged high air temperatures and shallow water depth is responsible for the unusually warm water temperatures that prevail in this area of the delta for as much as 5–6 months of the year. It is now well known that water temperatures of shallow bays on the northern Gulf coast exceed the air temperatures during the summer months. Dawson (1955) gives the latest information and cites previous papers.

The maximum and minimum temperature values observed during the survey are shown in Figure 4. Temperatures of 90° and over are common for most of the stations. In addition, a zone of over 100° temperatures occurs near the mouth of Blind Bay. These unusually high temperatures so early in the summer coincide for the most part with the extremely shallow water existing in the vicinity of stations G-22 and G-23 at the mouth of Blind Bay. Differences in temperature of one-half to one degree were found frequently in both bays between the surface and bottom. In general, the temperatures observed in Blind Bay were several degrees lower than Redfish Bay and are evidence of the much greater volume of river water that flows through Blind Bay.


Hingle Pass
Raphael Pass
Bull Bay
marsh
Paddy Bay
Bastian Lake
Pass a Loutre
Blind Bay
Southeast Pass
Northeast Pass
Northshore Bay
Cognevich Pass
Redfish Bay
Southeast Pass
marsh
Lookout I.
①
②
③
84 G28
83 G29
81 G24
83 G25
83 G26
82 G27
81 G23
82 G21
82 G22
82 G20
G30
82
81 G19
80 G14
81 G18
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80 G15
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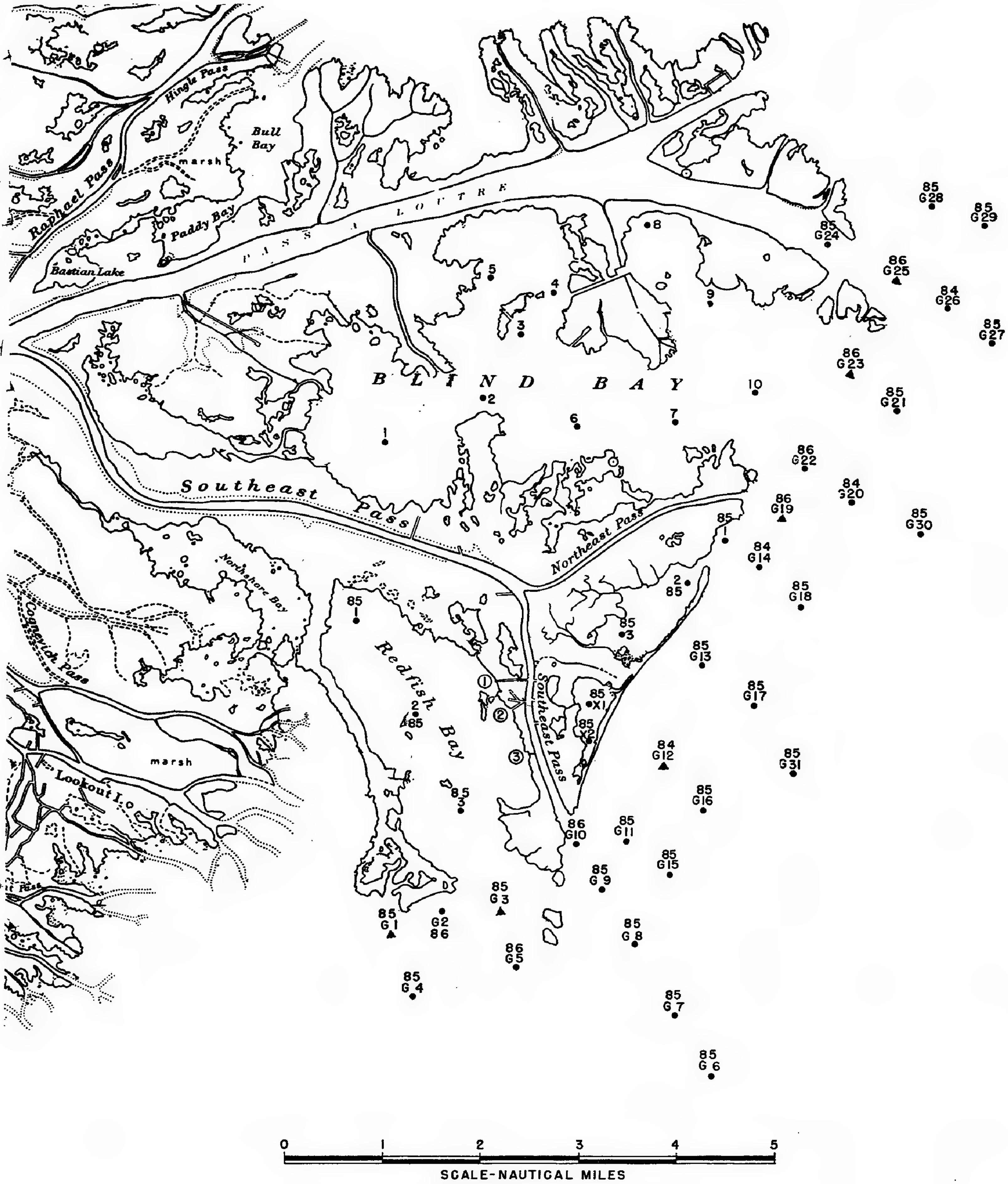
76 G10
77 G9
80 G3
78 G1
G2 81
80 G5
78 G4
77 G8
78 G7
78 G6
80
80
8 79
77 5
77 4
77 3
9 77
79 10
2 79
78 1
78 6
78 7
81
2 80
81 3
80
82 X1
82 X2
2 78
77 3
0 1 2 3 4 5
SCALE-NAUTICAL MILES

① & ③ EXISTING CANALS
② CANAL CUT BY HUMBLE

AVERAGE TEMPERATURE VALUES-MAY-5-JUNE 3, 1953
490 OBSERVATIONS - 49 STATIONS

FIGURE-2


Hingle Pass
Bull Bay
marsh
Raphael Pass
Paddy Bay
Bastian Lake
Pass a Loutre
Blind Bay
Southeast Pass
Northeast Pass
Northshore Bay
Cognevich Pass
marsh
Lookout I.
Redfish Bay
Southeast Pass
1 2 3 4 5 6 7 8 9 10
85 G28
85 G29
85 G24
86 G25
84 G26
85 G27
86 G23
85 G21
86 G22
84 G20
86 G19
85 G30
85 1
84 G14
2 85
85 G18
85 3
85 G13
85 G17
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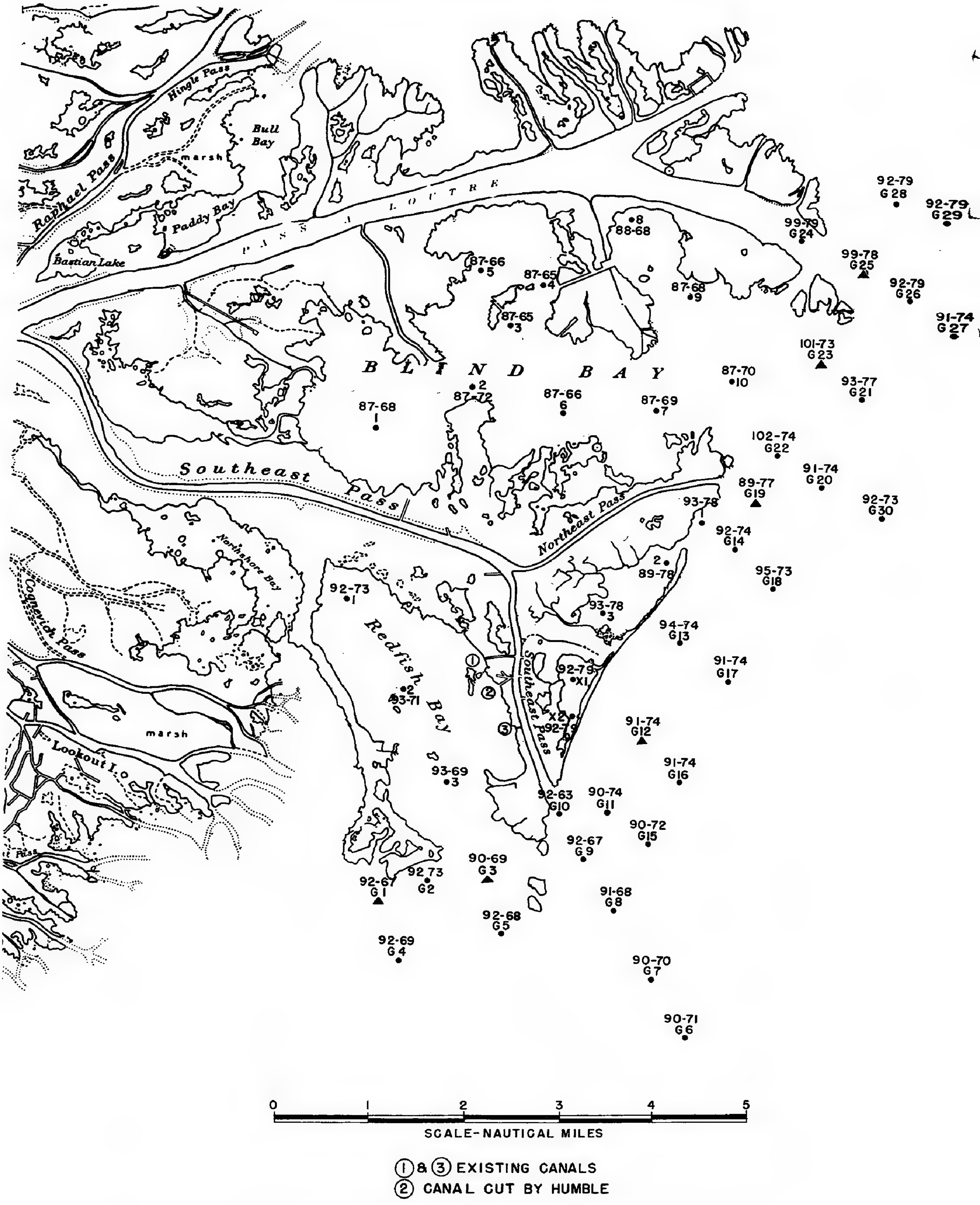
85 X2
84 G12
85 G31
85 1
2 85
85 3
85 G16
86 G10
85 G11
85 G15
85 G9
85 G3
85 G1
G2 86
86 G5
85 G8
85 G4
85 G7
85 G6
0 1 2 3 4 5
SCALE-NAUTICAL MILES

① & ③ EXISTING CANALS
② CANAL CUT BY HUMBLE

AVERAGE TEMPERATURE VALUES-JUNE 4-JULY 2, 1953
603 OBSERVATIONS - 39 STATIONS

FIGURE-3


Hingle Pass
Bull Bay
marsh
Raphael Pass
Paddy Bay
Bastian Lake
Pass a Loutre
B L I N D B A Y
Southeast Pass
Northeast Pass
Northshore Bay
Cognevich Pass
marsh
Lookout I.
Redfish Bay
Southeast Pass
92-79 G28
92-79 G29
99-79 G24
99-78 G25
92-79 G26
91-74 G27
101-73 G23
93-77 G21
102-74 G22
91-74 G20
89-77 G19
92-73 G30
93-78 1
92-74 G14
95-73 G18
94-74 G13
91-74 G17
91-74 G12
91-74 G16
90-74 G11
92-63 G10
90-72 G15
92-67 G9
91-68 G8
90-69 G3
92-68 G5
92-67 G1
92-73 G2
92-69 G4
90-70 G7
90-71 G6
88-68 8
87-66 5
87-65 4
87-65 3
87-68 9
87-70 10
87-72 2
87-68 1
87-66 6
87-69 7
89-78 2
93-78 3
92-73 1
92-79 X1
92-79 X2
93-71 2
93-69 3
①
②
③
0 1 2 3 4 5
SCALE-NAUTICAL MILES
① & ③ EXISTING CANALS
② CANAL CUT BY HUMBLE

MAX. & MIN TEMPERATURE VALUES - MAY 5 - JULY 2, 1953
1093 OBSERVATIONS - 49 STATIONS

FIGURE-4

Salinity

The effect of large quantities of fresh water discharged by the Mississippi and its distributaries on the salinity of the two bays and immediate offshore areas is evident in Figures 5 and 6. The general salinity pattern remains consistent over the period of the survey from month to month, although the isohaline contour values change with variations in the stage of the Mississippi. A wedge of high salinity Gulf water occurs close to shore, but it is surrounded to the north and south by less saline Gulf waters, which have been diluted by the fresh water issuing from Southeast Pass and Pass à la Loutre, as well as from Redfish and Blind Bays.

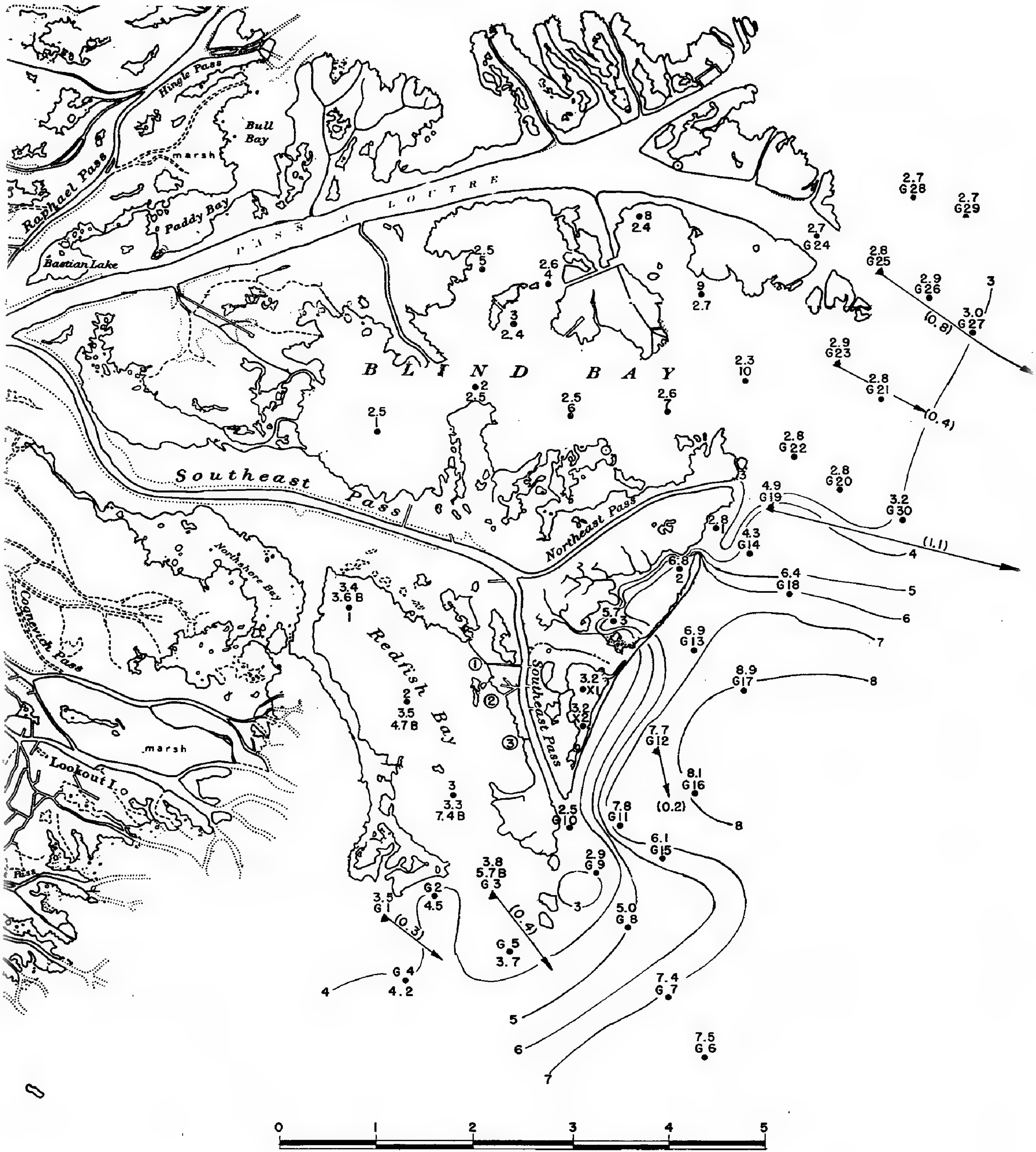
The configuration of the isohaline contours for the two periods, May 5 to June 3 and June 2 to July 4, is nearly the same, although the individual values average about six parts per thousand higher during the second period. This increase in salinity again can be attributed to the decrease in the volume of fresh diluting water available from the Mississippi during the second period. The higher salinity values correlate well with the fact that the average stage of the river dropped from 12 feet for the period, May 5 to June 3, (Figure 5), to approximately 8 feet for the period, June 4 to July 2, (Figure 6). The volume of river water discharged decreased markedly, but the path taken by the river water was the same.

The correlation between the stage of the Mississippi River and the salinity of coastal waters of the Gulf of Mexico has been demonstrated from information obtained from offshore drilling platforms (Geyer, 1950). The data for this study were gathered at seven drilling platforms during a 14-month period for a zone paralleling the coast for about 60 miles, approximately 6 to 8 miles offshore, and in water depths varying between 40 and 50 feet. This correlation (Figure 7) demonstrates that seasonal variations in the salinity of offshore coastal waters correlate with variations in the amount of water discharged by the Mississippi River. Since this effect makes itself felt so far offshore, it is not surprising that a correlation exists in the areas immediately adjacent to the distributaries of the Mississippi.

Other effects of the interaction of Mississippi River water and the saline waters of the Gulf of Mexico on the hydrography of the bays and adjoining offshore areas are demonstrated in Figure 8. In this figure, the maximum and minimum salinity values for the 1,093 salinity observations are plotted for the 49 locations used in this survey.

The volume of river water entering Blind Bay is so large that the maximum salinity observed during the period of May 5–July 2 was only 3.5 parts per thousand, and at several stations studied, fresh water was found, (Figure 8). On the other hand, the maximum salinity observed for the surface waters of Redfish Bay was generally about twice that observed in Blind Bay, or about 6 parts per thousand. In addition, the maximum salinity values recorded for the water at the bottom of Redfish Bay increases progressively from 6.8 at the head of the bay to 21.2 at the mouth. Similarly, minimum salinity values for Redfish Bay, both for surface and bottom waters, were never less than 2 parts per thousand. The generalizations made for Redfish Bay also apply to the two small unnamed bays situated between Redfish and Blind Bays along the edge of the delta.

During certain stages of the tide, more saline Gulf water enters along the bottom of Redfish Bay and the two smaller unnamed bays (Figure 8). Redfish Bay is deep enough so that the more dense saline Gulf waters tend to flow into the Bay below the lighter


Raphael Pass
Hingle Pass
Bull Bay
marsh
Paddy Bay
Bastian Lake
PASS A LOUTRE
BLIND BAY
Southeast Pass
Northeast Pass
Northshore Bay
Cognevich Pass
marsh
Lookout Lo
Pass
Redfish Bay
Southeast Pass
2.7 G28
2.7 G29
2.7 G24
2.8 G25
2.9 G26
3
3.0 G27
(0.8)
8 2.4
2.5 5
2.6 4
9 2.7
3 2.4
2.3 10
2.9 G23
2.8 G21
(0.4)
2 2.5
2.5 1
2.5 6
2.6 7
2.8 G22
2.8 G20
3
4.9 G19
3.2 G30
2.8 1
4.3 G14
(1.1)
4
6.8 2
6.4 G18
5
6
5.7 3
6.9 G13
7
3.4 3.6 B 1
8.9 G17
8
①
②
③
3.2 X1
3.2 X2
2 3.5 4.7 B
7.7 G12
8.1 G16
(0.2)
8
3 3.3 7.4 B
2.5 G10
7.8 G11
6.1 G15
3.8 5.7 B G3
2.9 G9
3.5 G1
G2 4.5
(0.3)
(0.4)
3
5.0 G8
G5 3.7
G4 4.2
4
7.4 G7
5
6
7.5 G6
7
0 1 2 3 4 5

SCALE-NAUTICAL MILES

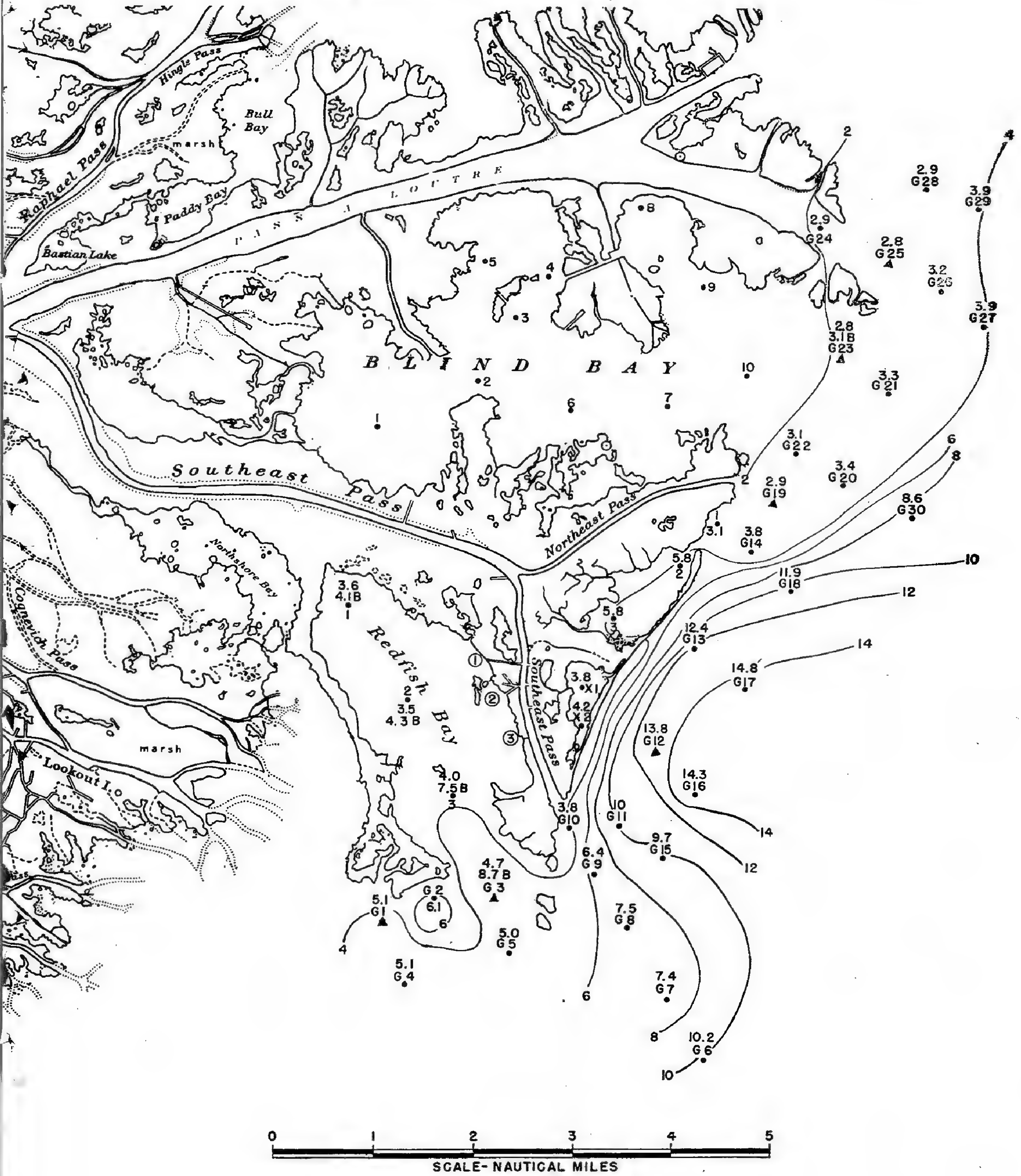
① & ③ EXISTING CANALS

② CANAL CUT BY HUMBLE

( ) AVERAGE CURRENT VELOCITY KNOTS
CURRENT DIRECTION PREDOMINANT
41 OBSERVATIONS 6 STATIONS

AVERAGE SALINITY VALUES-MAY 5-JUNE 3, 1953
(PARTS PER THOUSAND)
490 OBSERVATIONS- 49 STATIONS

FIGURE-5


Hingle Pass
Bull Bay
marsh
Raphael Pass
Paddy Bay
Bastian Lake
PASS A LOUTRE
BLIND BAY
Southeast Pass
Northeast Pass
Northshore Bay
Cognevich Pass
Redfish Bay
Southeast Pass
marsh
Lookout I.
2.9 G28
3.9 G29
2.9 G24
2.8 G25
3.2 G26
3.9 G27
2.8 3.1B G23
3.3 G21
3.1 G22
3.4 G20
2.9 G19
8.6 G30
3.1
3.8 G14
5.8
11.9 G18
12.4 G13
14.8 G17
3.8 X1
4.2 X2
13.8 G12
14.3 G16
3.6 4.1B
3.5 4.3B
4.0 7.5B
3.8 G10
10 G11
9.7 G15
6.4 G9
4.7 8.7B G3
G2 6.1
5.1 G1
5.0 G5
7.5 G8
5.1 G4
7.4 G7
10.2 G6
①
②
③
SCALE-NAUTICAL MILES
0
1
2
3
4
5

① & ③ EXISTING CANALS
② CANAL CUT BY HUMBLE

AVERAGE SALINITY VALUES-JUNE 2-JULY 4, 1953
(PARTS PER THOUSAND)
603 OBSERVATIONS - 39 STATIONS

FIGURE-6

fresh river water, as evidenced by uniformally higher salinity values of the bottom waters.

The fact that these conditions were not observed in Blind Bay can be explained by the availability of a very much greater volume of river water for Blind Bay from Pass a la Loutre and Southeast Pass. This contention is corroborated by the fact that the average current velocities observed at Stations G-19, G-23, and G-25 (Figure 5) are from 1 to almost 3 times as large as the average current velocity for Station G-3 located at the seaward entrance of Redfish Bay. This also explains the position of the 4 parts per thousand isohaline contour (Figures 5 and 6) which was found farther out in the Gulf away from the mouth of Blind Bay than from the mouth of Redfish Bay. During the period June 2–July 4 (Figure 6) when the volume of fresh water carried by the Mississippi was greatly reduced as compared with the period May 5–June 1 (Figure 5), the 4 parts per thousand isohaline contour extended about a mile into Redfish Bay. This is in contrast to its location of about a mile beyond the mouth of the bay during the previous month. However, the position of this contour is almost 2 miles beyond the entrance of Blind Bay (Figure 6) as compared with 2.5 miles offshore the previous month (Figure 5).

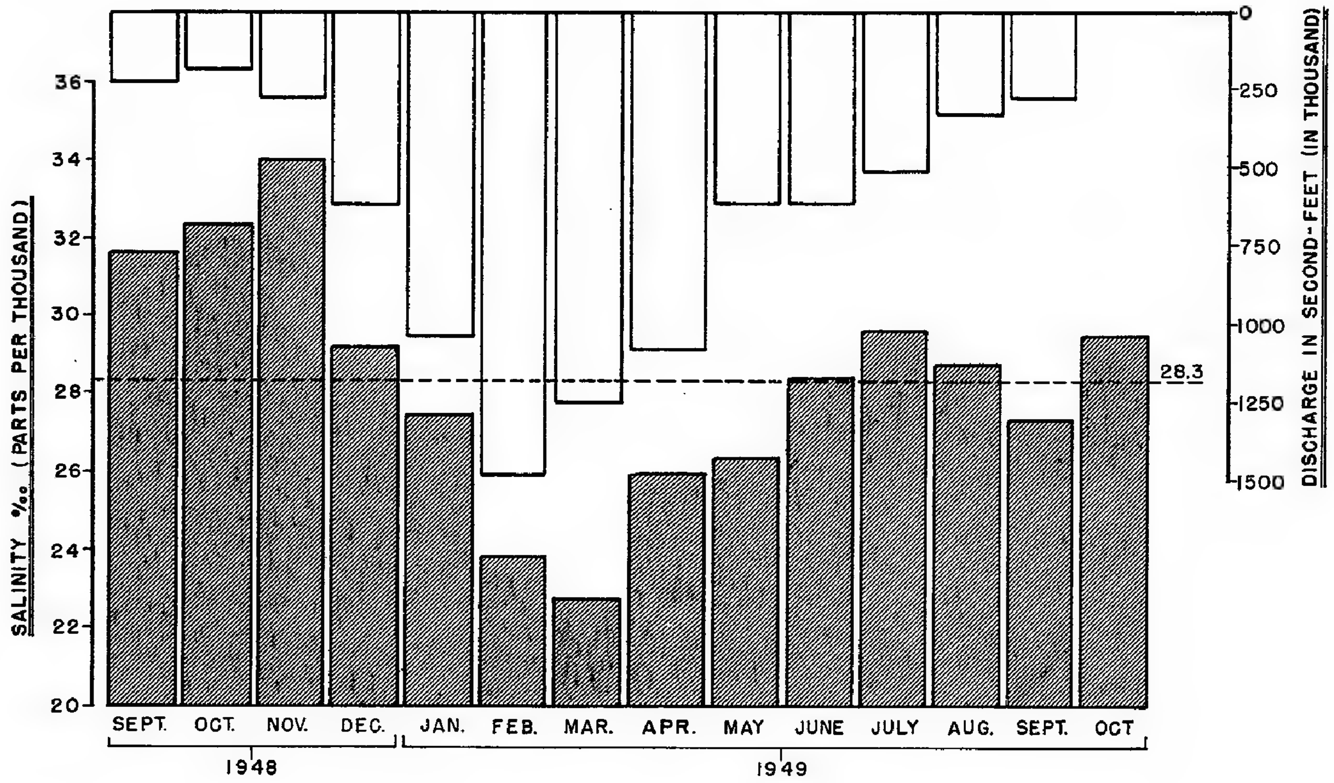
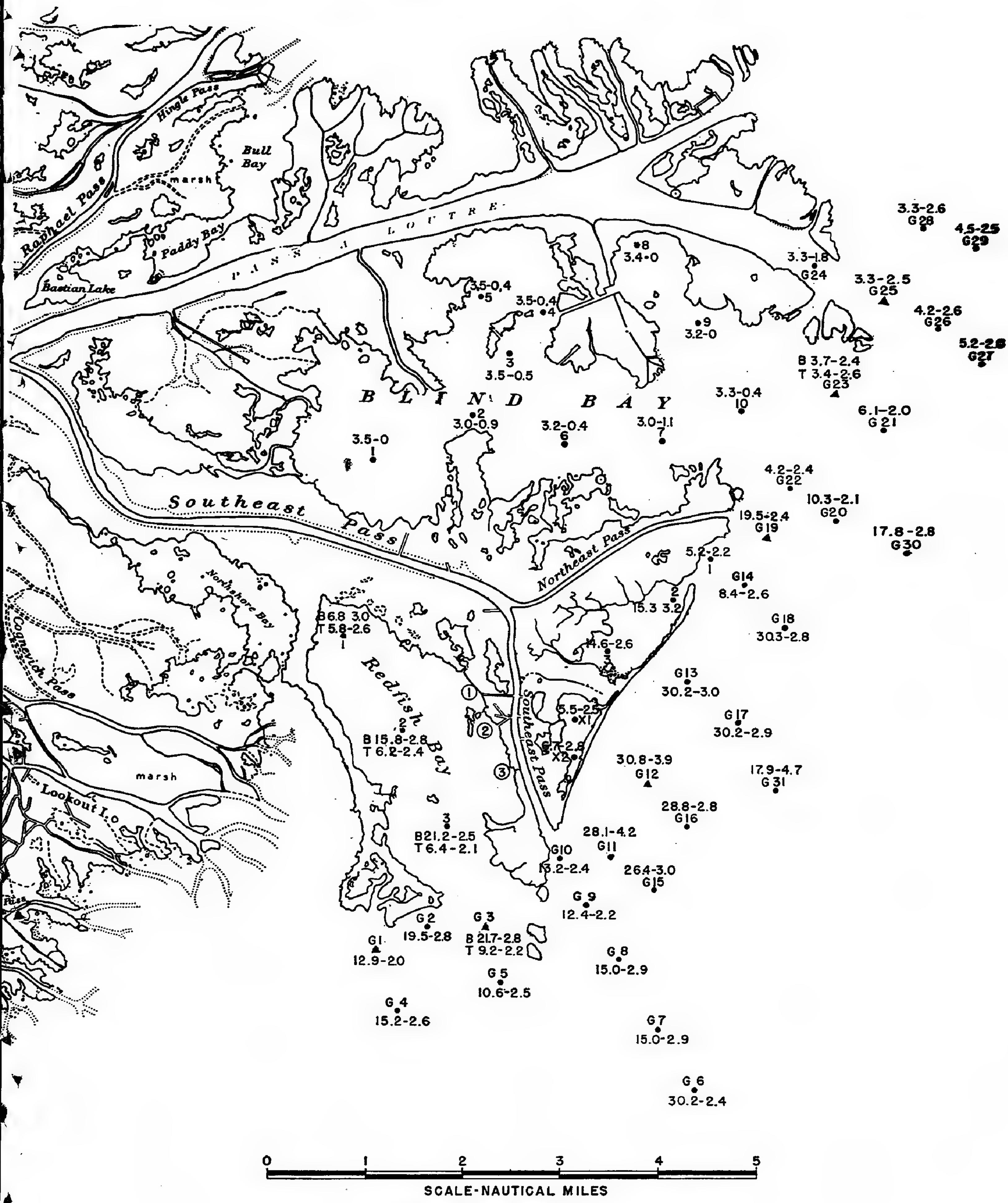


FIGURE - 7

COMPARISON OF MONTHLY AVERAGE SALINITIES IN COASTAL WATERS OF GULF OF MEXICO WITH DISCHARGE IN SEC.-FT. OF THE MISSISSIPPI RIVER AT VICKSBURG

Currents and Tides

The average current velocity and direction for the 6 current stations are based on a series of 41 observations (Figure 5). As would be expected, the predominant current direction at the mouths of the passes and bays is toward the Gulf. Stations G-12 was situated offshore between the passes, and the current flows in a southerly direction with an average velocity of 0.2 of a knot. The current direction and velocity of Station


Raphael Pass
Hingle Pass
Bull Bay
marsh
Paddy Bay
Bastian Lake
PASS A LOUTRE
BLIND BAY
Southeast Pass
Northeast Pass
Northshore Bay
Cognevich Pass
Lookout I.
marsh
Redfish Bay
Southeast Pass
3.3-2.6 G28
4.5-2.5 G29
3.3-1.8 G24
3.3-2.5 G25
4.2-2.6 G26
5.2-2.8 G27
8 3.4-0
3.5-0.4 5
3.5-0.4 4
9 3.2-0
3 3.5-0.5
B 3.7-2.4 T 3.4-2.6 G23
3.3-0.4 10
6.1-2.0 G21
2 3.0-0.9
3.2-0.4 6
3.0-1.1 7
3.5-0 1
4.2-2.4 G22
10.3-2.1 G20
19.5-2.4 G19
17.8-2.8 G30
5.2-2.2 1
G14 8.4-2.6
2 15.3 3.2
G18 30.3-2.8
B 6.8 3.0 T 5.8-2.6 1
14.6-2.6 3
G13 30.2-3.0
5.5-2.5 X1
G17 30.2-2.9
2 B 15.8-2.8 T 6.2-2.4
6.7-2.8 X2
30.8-3.9 G12
17.9-4.7 G31
28.8-2.8 G16
3 B 21.2-2.5 T 6.4-2.1
28.1-4.2 G11
G10 13.2-2.4
26.4-3.0 G15
G 9 12.4-2.2
G2 19.5-2.8
G3 B 21.7-2.8 T 9.2-2.2
G1 12.9-2.0
G 8 15.0-2.9
G 5 10.6-2.5
G 4 15.2-2.6
G 7 15.0-2.9
G 6 30.2-2.4
0 1 2 3 4 5
SCALE-NAUTICAL MILES

① & ③ EXISTING CANALS
② CANAL CUT BY HUMBLE

MAX & MIN. SALINITY VALUES – MAY 5 – JULY 2, 1953
1093 OBSERVATIONS – 49 STATIONS

FIGURE-8

G-1, just south of the entrance to Redfish Bay, is determined primarily by the flow of water from several of the minor distributaries located between South and Southeast Passes. The current direction at this station parallels the movement of the water of the distributaries, and the velocity is 0.3 of a knot.

Some idea of the comparative amounts of water flowing from the mouths of bays, as compared with the mouths of the distributaries, can be seen by comparing the difference in current velocity for the two locations (Figure 5). The average current velocity at the mouths of Redfish Bay and Blind Bay is 0.4 of a knot; whereas, off the mouths of Southeast Pass and Pass à la Loutre, the average current velocity is 1.1 and 0.8 of a knot, respectively.

The direction and velocity of currents in this area are effected in general by the astronomic and wind tides which prevail at the time the observations are made. During periods when the wind blows from the north at a high velocity for sustained periods of time, the waters in the marshes, bays, and bayous of this region are forced toward the Gulf of Mexico, leaving a minimum of water in the bays. Conversely, when strong winds, associated with storms in the Gulf, blow from the south, the Gulf waters are forced into the bays and marshes covering them at times to great depths. Although the range in astronomic tides is very low, about 2 feet, the storm tides associated with hurricanes have been known to reach a maximum of 10 to 12 feet in this general area.

CONCLUSIONS

Based on an analysis of the known hydrographic factors considered during the surveys, it is evident that the hydrography of Redfish and Blind Bays, at any given time, is dependent upon the prevailing stage of the Mississippi River. Shoreward movement of the saline Gulf waters associated with tide and wind action serves only to modify to a minor extent the major hydrographic patterns which are determined by variations in the stage of the river. These circumstances explain readily the fact that no changes in the hydrography of the area were detected during surveys conducted under comparable conditions before and after the cutting of the Humble canal.

ACKNOWLEDGEMENTS

This paper could not have been written without the cooperation of Dr. Gordon Gunter, Director of the Institute of Marine Science, and personnel of the Louisiana Division of Humble Oil & Refining Company, who obtained the field observations. They include Messrs. R. L. Askey, K. Pratt, and Lionel Despeaux. In addition, the writer also wishes to express his appreciation to Humble Oil & Refining Company for permission to publish this paper.

REFERENCES

(1936) Russell, R. J. Physiography of lower Mississippi River Delta. Louisiana Dept. Conservation Geol. Bull. no. 8, pp. 3–199.

(1939) U. S. Coast and Geodetic Survey, Chart H-6513.

(1948) Russell, R. J. Coast of Louisiana. Bull. Soc. belge Geol., Paleont, et d'Hydrol. vol. 57, pp. 380–394.

(1950) Geyer, R. A. The occurrence of pronounced salinity variations in Louisiana coastal waters. *Jour. Marine Research,* vol. IX, no. 2, pp. 100–110.

(1950) U. S. Coast and Geodetic Survey, *Manual of Current Observations,* Special Pub., no. 215, 86 pp.

(1952) Gunter, G. Historical changes in the Mississippi River and the adjacent marine environment. *Pub. Inst. Marine Sci.,* vol. II, no. 2, pp. 119–139.

(1955) Dawson, C. E. A contribution to the hydrography of Apalachicola Bay, Florida. *Pub. Inst. Marine Sci.,* vol. IV, no. 1, pp. 13–35.

A Study of the Fauna of the Pink Shrimp (*Penaeus duorarum* Burkenroad) Grounds in the Gulf of Campeche

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INTRODUCTION

Active exploration by members of the shrimping industry led to the discovery of two important new fishing grounds for pink shrimp *(Penaeus duorarum)* during 1950. The associated fauna was much different from that observed by the fishermen on the older white *(Penaeus setiferus)* and brown *(Penaeus aztecus)* grounds in the Gulf of Mexico. Consequently, preliminary studies were undertaken during 1951 on the pink shrimp grounds in the Gulf of Campeche in order to gather information on the distribution and relative abundance of animals caught in trawls. This study was related to a similar but more extensive survey of the brown shrimp *(Penaeus aztecus)* grounds (Hildebrand, 1954). Additionally, information on trawling grounds and areas and catch per unit of effort was compiled.

The Institute of Marine Science at Port Aransas, Texas served as the base of operation, and all field work was done aboard commercial trawlers. Unpublished information gathered during four years of work along the coast of Texas and Mexico is added where it clarifies the distribution or habitat of any species caught in the trawl. Except for a brief discussion of the flying fishes (Exocoetidae), the faunal discussion is limited to trawl catches and it is, therefore, not a complete survey of the bottom community. However, the results are comparable to trawl catch surveys of the brown and white shrimp grounds.

HISTORY OF THE EXPLORATION AND DEVELOPMENT OF NEW SHRIMPING GROUNDS IN THE GULF OF MEXICO

The shrimp fishery on the Gulf coast first developed in the bays and the lagoons. On the Gulf coast of the United States, except for peninsular Florida, shrimp were caught in large drag seines and castnets, while on the coast of Mexico shrimp were caught in fixed traps. This trap fishery still continues relatively unchanged and the greatest concentration of traps is in the north end of Laguna de Tamiahua. Shrimp taken by these methods can only be caught near shore or in very shallow water. Most of the shrimp caught were dried, although a few were marketed locally. At a later date, canning plants were supplied by drag seines. However, in Mexico most of the trap-caught shrimp are still dried.

The introduction of the otter trawl sometime between 1912 and 1915 (Anderson *et al.*, 1949) in Louisiana freed the fishermen from dependence on the seasonal abundance of shrimp in shallow water. For a number of years the demand for shrimp was entirely supplied by the production of shrimp from the bays and shallow water of the open Gulf. In 1938 the large scale production of jumbo white shrimp on the Shipshoal grounds off Morgan City, Louisiana began and the resultant national publicity helped create new outlets for the shrimp catch. The size of the Gulf shrimp fleet increased greatly, and a number of large offshore trawlers were built. Although the addition of new boats to the fleet was stopped during World War II, it can be stated that all shrimping grounds for white shrimp in the northern Gulf of Mexico were known and were being exploited shortly after the end of the war.

In 1946, the crew of the "Sovereign", an 84 foot boat owned by Major J. A. Pullen, discovered an enormous concentration of white shrimp off Carmen in the Gulf of Campeche. These fishing grounds had been previously explored by the Japanese in 1936 and 1937, but their location was unknown to the Louisiana boat owners. After the return of the "Sovereign" a number of trips were made to the fishing grounds in the Gulf of Campeche. However, this shrimp "boom" was dampened when Mexican authorities refused to license American boats for fishing in territorial waters, and a number of American fishermen were detained in Mexican ports on December 28, 1946. Smaller concentrations of white shrimp were discovered elsewhere along the Mexican coast, and although some fishing in Mexican territorial waters continues, the production by American boats is very small.

The large trawlers were concentrated at Port Isabel during the spring of 1947 and according to a news release in the Southern Fishermen, 500,000 pounds of white shrimp were unloaded in Port Isabel during week-end of April 20, 1947. Since out-of-state trawlers could not be licensed in Texas at that time, extensive areas along the Tamaulipas coast were explored.

The decline of the white shrimp production has been discussed by Gunter and Hildebrand (1953). The decline occurred shortly after the end of the war, when the demand for shrimp was high and previous high earnings of the fleet had attracted many new fishermen.

Although brown shrimp had been sold for many years, most of them were dried, canned or peeled. There was considerable consumer's resistance to the brown shrimp because of the color, and the quantity that could be sold on the fresh market was very small.

During the first half of 1947, the production of shrimp was very low along the Texas coast and often the boats would bring in mixed catches of white and brown shrimp. The proportion of whites and browns (50 per cent browns or more) was such that it was impossible to market them in one package. Mr. John Nelson of Aransas Pass was approached by a group of fishermen who wanted to set up a cooperative marketing agency for their shrimp. He acted as a broker for these owners, who were anxious to push the sale of brown shrimp, until the cooperative was officially established during February, 1948. The first carload of brown shrimp was shipped to San Francisco during August, 1947. The brown shrimp were carefully graded to uniform size and shipped at cost to develop the market. Mr. Nelson and the cooperative handled most of the brown shrimp that were sold the first year, and after the first six months the market was strong enough to handle all the brown shrimp produced by members of the cooperative.

It can be categorically stated that almost ninety per cent of the production of brown shrimp during 1947 and 1948 were caught along the Texas coast with the greatest production at Aransas Pass. The rich 24–10 shrimp beds, although discovered during 1947, did not figure prominently in the brown shrimp catch until 1949 when they dominated the catch.

Brown shrimp production developed somewhat later off Mississippi, Alabama and Louisiana because the owners of the large trawlers did not find brown shrimp so abundant as on the 24–10 grounds. However, the shrimping grounds offshore were well-known to many of the fishermen. The offshore fishery developed during June, 1950, when large trawlers from the Texas fleet brought the first sizable landings of large brown shrimp into Alabama ports. The discovery of all commercial fishing grounds in the Gulf of Mexico are the results of the activities of the shrimp fishermen themselves.

The last major discovery of a commercial brown shrimp ground was the Obregon grounds. Commercially valuable concentrations were apparently exploited for the first time during the full moon of April, 1951. For several months afterwards the boats would leave Campeche for Obregon to fish for brown shrimp during the full moon. However, fishing pressure became so great in the Gulf of Campeche that fishermen informed me that it soon became difficult to prove that fishing was any better during one phase of the moon than another.

After the discovery of the Obregon (brown shrimp) grounds, the development of small "pockets" in the area between Punta Jerez and Alvarado, Mexico began. The largest area of trawlable bottom was found in the region around Lobos Island (Hildebrand, 1954). Still later the fishermen actively explored and exploited fishing grounds off Galveston and Freeport. During the winter of 1954–55 many fishermen were operating in depths of 30 to 50 fathoms off Freeport and Galveston.

Pink shrimp were first described by Burkenroad (1939). He gives the range as extending from Cape Hatteras, North Carolina to Sabanilla, Colombia and the west coast of Africa. Nearly all his records from the Gulf of Mexico were from the west coast of Florida. He lists only Vera Cruz in the western Gulf. Although the details of its distribution in the Gulf of Mexico are not yet known, pink shrimp have not authoritatively been reported between the mouth of the Mississippi and the meridian of Galveston, and very little is known about their distribution along the east coast of Mexico.

Burkenroad (1949) described a 10 year-old fishery between Core Sound and Beaufort Inlet in North Carolina. Here seventy channel nets were fished on the night ebb tide in May, June and July. The annual production of these nets is around 100 tons, and although a portion of brown shrimp *(Penaeus aztecus)* is present, the catch is chiefly immature *Penaeus duorarum.*

Undoubtedly small pink shrimp have supported small fisheries in other bays along the Gulf coast, particularly a bait fishery along the west coast of Florida, but the landings have never been great.

In the northern Gulf the fishery for pink shrimp has been insignificant, and although few data are available, it is probable that it is less than one per cent of the catch (Hildebrand, 1954). Springer (1952) stated that at times the Mississippi fleet landed as much as 30 per cent pink shrimp. However, he stated that in 1953 and 1954 the fauna had changed and less than one per cent pink shrimp were landed (Springer and Bullis, 1954).

The most highly publicized and the first really major development of a pink shrimp fishery occurred in 1950 with the exploitation of the Tortugas shrimp grounds. Idyll (1950) gives an account of the discovery of the pink shrimp grounds off Key West and Tortugas and the following summary is from that account.

Exploratory fishing in the Tortugas area was begun by S. Salvador and Sons associated with Mr. E. L. Peterson during September, 1949, following accounts of successful night fishing for grooved shrimp in Texas. Results were encouraging and commercial operations began in January, 1950. When the discovery became generally known, rapid expansion followed and during February, 1950 an estimated 2,117,000 pounds (whole shrimp) were landed. Two hundred and fifty to three hundred boats were fishing there by March 1, 1950. The fishing grounds are located north of a line drawn from Key West to Loggerhead Key in the Dry Tortugas group. They are approximately 70 miles long by 10 to 15 miles wide. The bottom is covered by fine calcareous sediments ("coral mud") with some coral obstructions.

However, the large fleet dispersed by the end of March, 1950 and there has been a steady though not spectacular production since that time. The Florida Landings give production figures of 11 million pounds in 1950 and 17 million pounds in 1953.

TABLE 1

Production of Penaeus duorarum Burkenroad in the Gulf of Campeche and on the Tortugas Grounds by Area of Landing*

Year	Campeche		Tortugas
	Texas	Florida	Florida
1950	1,500‡	....	11,270
1951	5,530	7,005	19,465
1952	460	23,000	11,460
1953	not available but less than 1952	32,320	17,420
1954	not available but less than 1952	19,511	17,500

* The Texas landings are from the Fishery Market News Service except the estimate for 1950 which is my own. Florida landings are from the Fish and Wildlife Service and from the "Florida Landings." An unknown quantity of brown and white shrimp are included in the "Florida Landings" from Campeche Bank, and these landings may include other areas besides the Gulf of Campeche. It is known that considerable quantities of shrimp were bought from Mexican trawlers at sea and landed in Florida ports by Florida boats. The Tortugas landing for 1954 is based on a news release by Dr. C. P. Idyll. Statistics of Mexican landings are not available. Trade journals reports landings of 15 to 20 million pounds of Browns, Whites and Pinks in Mexican ports in the Gulf of Campeche.

‡ Thousands of Pounds.

Although the pink shrimp grounds off Campeche were prospected by the Japanese in 1936–37, they were unknown to Texas fishermen. John Wiech, a man closely associated with shrimp developments in the Gulf of Campeche, informed me that probably the first shipment from the banks was made by Sandy Cole in 1947 when he sent 1,500 pounds to Brownsville. However, the shrimp buyer in Brownsville requested that no more be sent because of marketing difficulties. Exploitation of the Campeche Bank shrimp fishery started when Adam Smith's trawler, the "Oro Lobo", brought a load of pink shrimp into Brownsville on May 23, 1950. Because of a shortage of ice the catch was only 30 barrels, but the boat captain knew that he had located extensive new beds of shrimp. On the next trip the "Oro Zorro" and "Oro Lobo" had cargoes of 120 barrels each. The secret of the new grounds became common knowledge, and a large number of fishermen started making the trip across the Gulf to new fishing grounds.

The production figures of this fishery are not readily accessible but the writer has reason to believe that the estimates of landings at Texas ports are too low. The discovery and development of the Campeche fishery was at first entirely a Texas operation. The first Florida based fishermen apparently arrived on the grounds during January, 1951, but by April, 1951 the majority of the boats were based in Florida. However, some of the boats fishing the grounds were transients from New England. A record breaking run of brown shrimp during the fall of 1951 kept most Texas fishermen away from Campeche Bank, and the Florida fishermen have produced over 90 per cent of the shrimp from the banks since that time.

Pink shrimp landings are given for both Tortugas and Campeche Grounds. However, Campeche catch statistics include catches of brown and white as well as pink shrimp. Furthermore, there may be landings from other fishing areas on the Gulf coast including Louisiana and Texas. One will note that there has been a very definite decline in the Campeche landings in Florida, but whether this actually represents a decline in pink shrimp is not known. One fisherman, who regularly fishes the brown shrimp grounds off Obregon, stated that the fishery was almost a complete failure during the last half of 1954, and it may be that much of the decline is due to a decrease in brown shrimp.

METHODS AND EQUIPMENT

The same plan was followed as in the investigation of the brown shrimp *(Penaeus aztecus)* fishery (Hildebrand, 1954). A fishing log was composed for the catch in each trawl haul and the limited amount of pertinent data that could be gathered from commercial shrimping operations.

All the trawling reported in this paper was done during the months of February and July, 1951. I left Aransas Pass aboard the "San Jacinto" at noon on February 3, 1951 and after an elapsed time of 16 days at sea, I returned to Aransas Pass at noon on February 19, 1951. Eighty-eight hours were spent trawling for shrimp between 5 p.m. on February 6, 1951 to 8 p.m. on February 16, 1951. However, fishing was stopped at 8 p.m. on February 7, 1951 because of bad weather and we did not resume fishing until 6 p.m. on February 9, 1951. Therefore, less than twenty-five per cent of the time at sea was spent fishing. On my second trip to the Campeche Banks I left Aransas Pass on the afternoon of July 24, 1951 aboard the "Texas Clipper" and I returned to Aransas Pass on August 8, 1951. However, we fished only 18 hours on Campeche Bank during the nights of July 27–28, 1951, and the remainder of the fishing time was spent trawling off Obregon, Mexico on brown shrimp beds.

The catch in each drag was examined by the writer when it came aboard. An attempt was made to record all species of fishes, shrimp and the larger invertebrates in each drag. This had to be accomplished without interfering with the rapid and efficient operation of the commercial trawlers. The species list was compiled by rapidly checking the catch immediately after it was dumped on deck, sorting from one-fourth to one-tenth of the catch in the normal commercial manner and finally checking the trash for species not listed by the preceding two methods.

The commercial catch of shrimp was recorded by baskets for each drag and this was converted to pounds per basket by dividing the number of baskets of shrimp into the total pounds of shrimp landed on arrival in Aransas Pass. Large and conspicuous organisms were recorded numerically in each drag. During February, 1951, five drags were recorded numerically by counting a portion of the catch and during July two drags were so recorded. In the remaining trawl hauls, a species record was kept with notations on abundance. Usually three or four species of fishes completely dominated the catch and they were ranked in order of abundance.

In order to check field identifications a preserved collection of 580 fishes and several hundred invertebrates was added to the collections of the Institute of Marine Science. If it was found that two or more species were confused in the field, such data were grouped.

All work was done aboard two commercial shrimp trawlers. The "San Jacinto", a wooden trawler built in Biloxi, Mississippi, had joined the shrimp fleet during July, 1950. The "San Jacinto" was 62.5 ft. long and 21.05 ft. across the beam. It was powered by a 130 horsepower Caterpillar diesel engine. The net measured 120 feet along the lead line. The lead line was very lightly leaded; otherwise the net was the standard Texas flat-net (otter trawl). The captain of the "San Jacinto", J. F. Allen, had been a shrimp fisherman for over forty years. He started in Georgia and followed the areas of best shrimping to Morgan City, Louisiana, later to Texas and finally to Campeche.

The "Texas Clipper", 66 ft. in length and 20 ft. across the beam was a steel trawler. The vessel was powered by two 165 horsepower General Motors diesel engines. The trawl measured 120 feet along the lead line, but the leads had been replaced by a "jumper" chain tied about 12 inches in front of the lead line. Lewis Deshotel was owner and captain of the "Texas Clipper". He was an experienced shrimp boat captain who had fished extensively in the western Gulf.

The shrimp fishery for pink shrimp is operated in much the same manner as for brown shrimp except that it is confined to shallower water. Apparently no pink shrimp are caught commercially beyond 25 fathoms, and almost all are caught in the six to eighteen fathom zone, at least by American trawlers. The size of the Mexican fishery in waters shallower than five fathoms is not known. Nearly all fishing is at night; the first drag is started around sundown and fishing continues until shortly after sunrise. There are exceptions, however, for we once found the fishing better during the daytime than it was either the preceding or following night. The reason for this is not clear, but it is possible that it was related to a heavy ground swell.

During February, the length of the drags varied from fifty minutes to two hours. The length of the drags was conditioned by the large catches of shrimp and "trash" and unfamiliarity with the new fishing grounds.

Many shrimp boats congregated on the Campeche Banks during February and usually we fished with the fleet. Several times during February I counted all the running lights visible from the deck of the "San Jacinto" and these counts varied from 25 to 53. During July, there were very few boats and I never saw more than seven running lights at any one time.

During the first six months of the Campeche fishery, fishermen from Aransas Pass, Texas figured about 16 days for a "trip" (100 to 140 barrels of shrimp) to the Campeche Banks and return. This included ten nights fishing on the banks and six days for the round trip across the Gulf. However, trips were sometimes prolonged by sending home part of the catch with a boat returning without a full load. During March, April and

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EXPLANATION OF FIGURE 1

This map is based on data supplied by Mr. John Wiech, an experienced navigator and shrimp fisherman in the Gulf of Campeche. It shows the fishing grounds and principal areas of production of shrimp in the Gulf of Campeche from August, 1950 to August, 1951.

Area 1.	Pink shrimp; size 21/25 count; abundant during hurricane season (August to November, 1950).
Area 2.	Pink shrimp; size 15/20; total fishing area small and consisting of small holes among the big logger-head sponges; areas buoyed when fishing.
Area 3.	Pink shrimp; big producing area from November 1, 1950 to January 1, 1951; bottom with occasional flat rocks, washboard topography but with fewer conchs than Area 4.
Area 4.	Pink shrimp abundant; also the area with the greatest concentration of conchs.
Area 5.	"Quick sand" and mud lumps; not fished.
Area 6.	Pink shrimp; size mostly 25/30 count; most of pink shrimp produced here from January to June, 1951.
Area 7.	White shrimp; during February and March, 1951 enormous quantities of white shrimp were encountered here; some boats produced 60 to 70 barrels a day and production was slowed by inability to handle the shrimp faster.
Area 8.	White shrimp; a few scattered boats found large concentrations of white shrimp during February and March, 1951.
Area 9.	Brown shrimp; heavy concentration of large brown shrimp.
Area 10.	Brown shrimp; smaller than Area 9; most shrimp 20/30 count.
Area 11.	White shrimp; mixed sizes but mostly 20/25 count during August, 1951.
Area 12.	Pinks merge with brown shrimp, but production so slight during 1950–51 that no boats fished the ground. Bottom very good.
Area 13–14.	Pear and New Bank. 18 fathoms; rough bottom but plenty of shrimp. Some fishing by a few boats.

May, 1951 refrigerated "buy" boats operated on the banks and they bought the catch directly from the fishermen. A few refrigerated trawlers operated for a month or more on the banks, but they caught only a small portion of the total catch from the banks. Later, when the Florida fishermen completely dominated the fishery, small trawlers would remain a month or more on the banks and send their shrimp home by other trawlers, usually on a boat belonging to the same company.

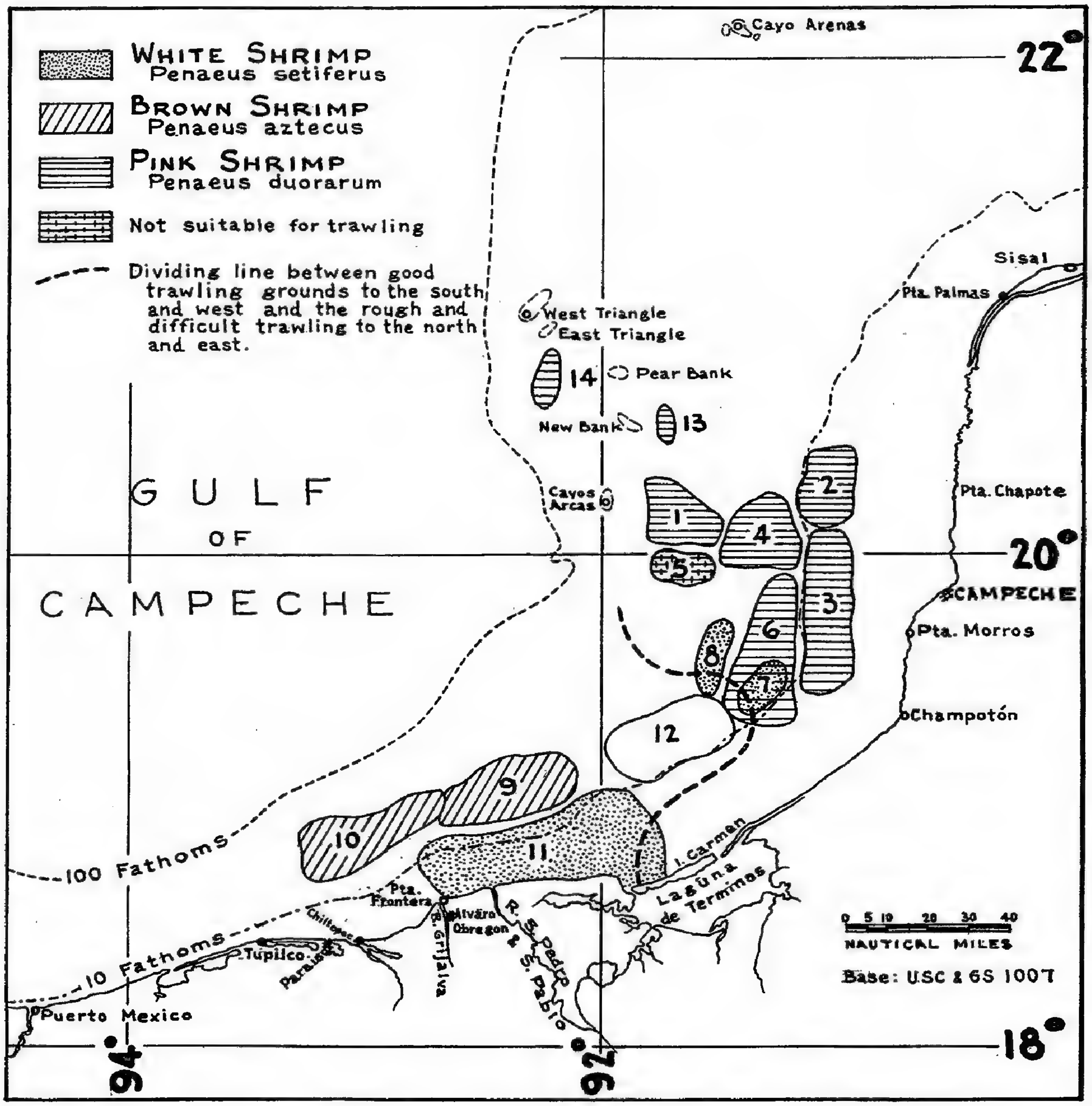
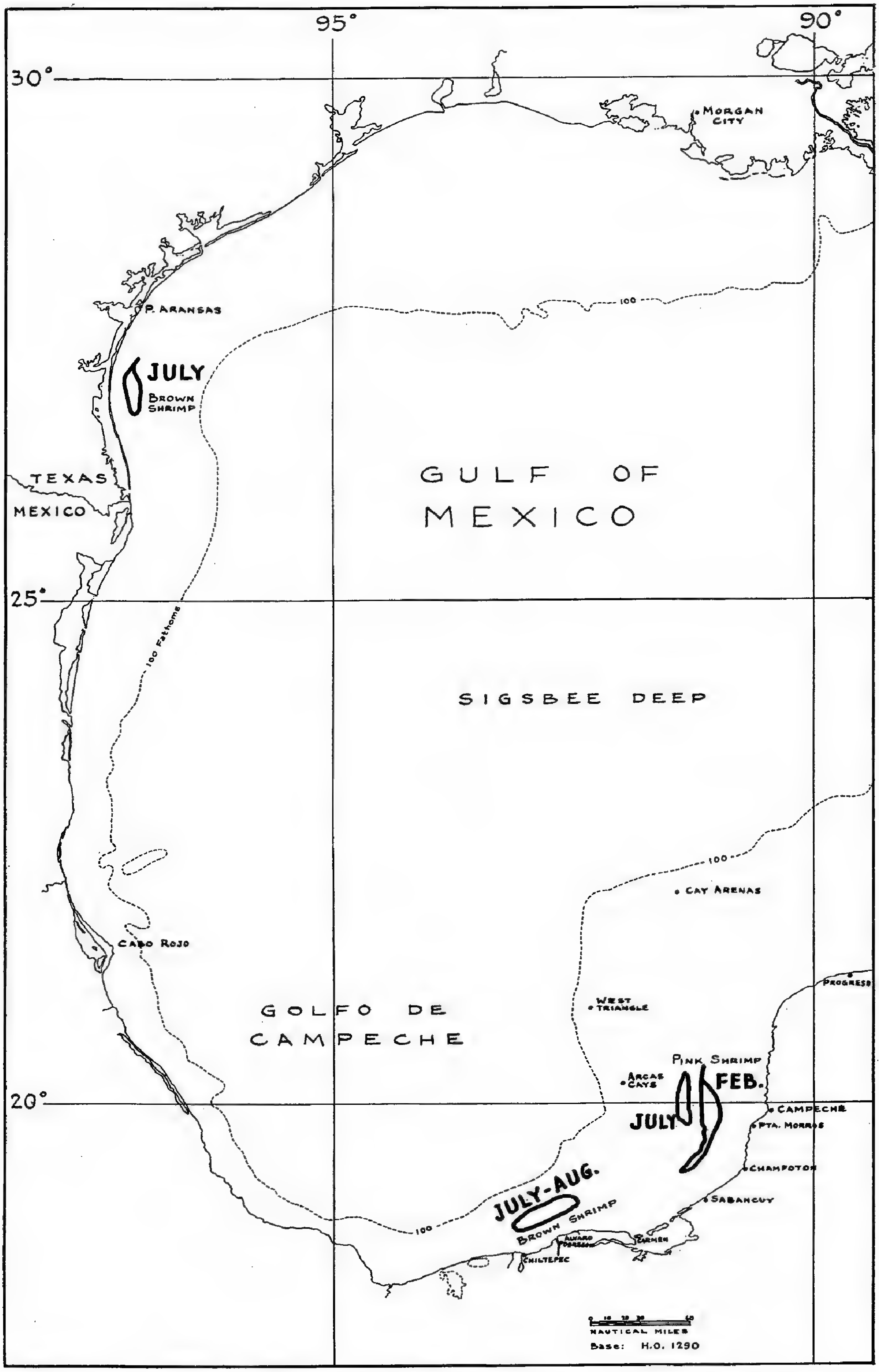

WHITE SHRIMP
Penaeus setiferus
BROWN SHRIMP
Penaeus aztecus
PINK SHRIMP
Penaeus duorarum
Not suitable for trawling
Dividing line between good trawling grounds to the south and west and the rough and difficult trawling to the north and east.
Cayo Arenas
22°
Sisal
Pta. Palmas
West Triangle
East Triangle
Pear Bank
New Bank
Cayos Arcas
GULF
OF
CAMPECHE
Pta. Chapote
20°
CAMPECHE
Pta. Morros
Champotón
1
2
3
4
5
6
7
8
9
10
11
12
13
14
100 Fathoms
10 Fathoms
I. Carmen
Laguna de Terminos
Pta. Frontera
Alvaro Obregon
R. Grijalva
R. S. Pedro & S. Pablo
Chiltepec
Tupilco
Paraiso
Puerto Mexico
0 5 10 20 30 40
NAUTICAL MILES
Base: USC & GS 1007
18°
94°
92°

FIGURE 1. Major shrimping grounds in the Gulf of Campeche (August, 1950 to August, 1951).

AREAS FISHED

Important commercial fishing grounds for the pink shrimp *(Penaeus duorarum)*, the brown shrimp *(Penaeus aztecus)* and the white shrimp *(Penaeus setiferus)* exist in the Gulf of Campeche in contiguous areas. Undetermined resources of a different type of shrimp (*Macrobrachium* spp.) occur in the rivers draining the rain coast from Coatzacoalcos to Carmen, Mexico. Although there is some overlapping in range, the



95°
90°
30°
25°
20°
MORGAN CITY
P. ARANSAS
JULY
BROWN SHRIMP
TEXAS
MEXICO
GULF OF MEXICO
100
100 Fathoms
SIGSBEE DEEP
100
CAY ARENAS
CABO ROJO
WEST TRIANGLE
GOLFO DE CAMPECHE
PROGRESO
PINK SHRIMP
ARCAS CAYS
FEB.
JULY
CAMPECHE
PTA. MORROS
CHAMPOTON
SABANCUY
JULY-AUG.
BROWN SHRIMP
100
ALVARO OBREGON
CARMEN
CHILTEPEC
0 10 20 30 50
NAUTICAL MILES
Base: H.O. 1290

FIGURE 2. Location of trawling operations conducted by the writer on the pink shrimp *(Penaeus duorarum)* grounds and comparative drags on the brown shrimp *(Penaeus aztecus)* grounds in the Western Gulf of Mexico.

bulk of the catch of each species comes from distinct areas. While the different species vary seasonally in abundance, some evidence has been accumulated which indicates that the peaks in abundance of the various species may vary from one year to another, presumably as a result of changes in the physical environment. One wonders if the reputed great decline in the brown shrimp fishery off Obregon during 1954 could be related to the very heavy rainfall in the region from Tampico to Carmen during 1954.

Here we are concerned only with the pink shrimp grounds on Campeche Banks and not with the brown and white shrimp grounds. However, the statistics of the "pink" shrimp landings in Florida include several species and at least all the area in the Gulf of Campeche from the Chiltepec shell ridge to the easternmost edge of the banks.

Lynch (1954) has characterized Campeche Banks as similar to the shelf off the west coast of Florida. In other words, it consists of hard rock, chiefly limestone with a thin veneer of detrital sediments that in local areas fill some of the depressions. Hedgpeth (1954) by reviewing the literature and examining hydrographic charts recognized four major bottom communities in the Gulf of Mexico. These are the coral community, the sponge community (possibly only a sub-community of the coral grounds), the shrimp community and the oyster community, and he maps areas where the coral and shrimp communities occur on Campeche Banks.

Local patches of coral are known to be particularly prevalent on the northern part of the banks. Such areas are not trawlable and this community was not sampled. Pink shrimp are known to be present on sponge (chiefly loggerhead sponges, *Spheciospongia vesparia*) grounds, but areas heavily infested with this sponge are not trawlable. Several times this community was sampled with the shrimp trawl during this investigation, but each time the net was damaged and only a small catch was landed.

A glance at the explanation of Fig. 1 will show how varied the shrimp grounds are on Campeche Bank. The information on which the chart was based was supplied by Mr. John Wiech, and it relates to the shrimp fishery from July, 1950 to August, 1951. Although in all cases the sediment is predominantly calcareous, it may vary from fine calcareous mud to shell "piles". The shell "piles" are composed of many old and broken shells, as well as many live large conchs and shells occupied by hermit crabs and octopuses. The map in Fig. 1 does not include all the pink shrimp grounds, but only the most important ones.

It is known that even in the early days of the fishery, shrimp fishermen swarmed over the banks seeking trawlable bottom outside the area of the main fishery. Trawlable areas were found, some of them being so small that it was necessary to buoy each end before they could be worked, but most of these locations have not been mapped. It is not known how much such areas contribute to the total shrimp catch, nor how the catch per unit of effort relates with the main shrimping grounds. However, it can be stated that the banks have been crossed and crisscrossed by trawlers so many times that all of these trawlable patches are known to one or more fishermen.

DISCUSSION OF THE FAUNA BY SPECIES

Invertebrata

Only the large and conspicuous invertebrates are discussed in this report. However, the many sponges, large conchs, ascidians and algae caught in the trawl supported an abundant array of small invertebrates such as small snails, xanthid crabs, crangonid shrimp and innumerable encrusting organisms. Such a varied fauna of small invertebrates is never encountered in the trawl catches on the mud bottom off the coast of Texas.

Porifera

Sponges are notoriously hard to identify in the field because of the great variability in their external appearance, depending upon ecological conditions such as type of substratum, crowding, etc. Nevertheless, sponges were often noted as abundant and in some areas they are the dominant organisms. Large areas of Campeche Bank, particularly the northern portion, are not trawlable because of the abundance of loggerhead sponges, *Spheciospongia vesparia.* In the early days of the new fishery for pink shrimp much gear was lost or torn. For example, the first drag of the "San Jacinto" in 8½ fathoms northwest of Campeche, Mexico resulted in a badly torn net and the catch consisted chiefly of loggerhead sponges.

A few of the common sponges on Campeche Bank were dried and sent to Dr. Willard Hartman for identification. He found that seven sponges were common and well known species in the waters off Florida and the West Indies. Two specimens apparently represented undescribed species. He lists the following sponges:

Oligoceras collectrix hemorrhages de Laubenfels
Axinella polycapella de Laubenfels
Axinella sp.
Haliclona rubens (Pallas)
Haliclona sp.
Thalysias juniperina Lamarck
Ircinia ramosa de Laubenfels
Ircinia campana (Lamarck)
Higginsia strigilata (Lamarck)

I noted both *Axinella polycapella* and *Haliclona rubens* as common and conspicuous sponges in some of the trawl hauls in 7 to 10 fathoms of water.

Coelenterata

Coelenterates were not often recorded during this study, although at times they were abundant. Sea anemones and solitary corals attached to shell and other objects from the substratum were common. Although large areas of coral bottom have been mapped on the northern part of Campeche Bank (Heilprin, 1890), such grounds, of course, could not be investigated with a shrimp trawl. However, some of the material that the shrimp fishermen were calling coral proved on examination to be calcareous algae. Perhaps the most striking feature was the absence or rarity of alcyonarians in the trawl catches.

Mollusca

In contrast to Texas waters, shell "banks" often prove very productive on Campeche Bank. Fishermen have modified their trawls by adding a "jumper or tickler chain" tied about 11 inches in front of the foot rope and thereby dispensing with leads on the foot rope. At the beginning of the fishery, leads were used on the foot rope, but often gear was lost under the accumulated burden of numerous conchs. Although comparative data are lacking, it is likely that the catch of shrimp is not materially reduced by using a "jumper" chain instead of leads.

The inadequacy of the shrimp trawl as a mollusk dredge has been previously discussed (Hildebrand, 1954), but nevertheless trawls will capture the larger motile forms that live on the surface. Furthermore, many of the smaller mollusks that live in sponges or attach themselves to other large organisms are captured. However, I did not record the smaller mollusks, and since it has been estimated that over 95 per cent of the marine mollusks are under one-half inch in length, the following species should not be considered as comprising a check list of the molluscan fauna. However, it is comparable to mollusks taken by the same method off the northern Gulf coast.

Undoubtedly, the otter trawl will affect most of the animal community on shell bottom. Old rotten shells are fragmented quickly and many of the larger slow growing gastropods and pelecypods are carted away to curio shops, or killed by being repeatedly trawled and dumped. Possibly, the introduction of the "jumper" chain and "bottomless trawls" will keep such damage to a minimum. Certainly the number of shells trawled with a jumper chain is much less than the number taken by a heavily leaded line.

Not all the bottom off Campeche supports dense accumulations of conchs. Some of it is a clear white calcareous sand, from which very few large shells are taken in a trawl. One particularly favorable shrimping grounds is in 7 to 9 fathoms of water off Punta Morros.

I took notes on the more common large mollusks during the February trip to Campeche Bank. However, most of my data are concerned with species enumeration and general statements concerning the abundance or rarity of species encountered in the trawls. Numerical data were collected during seven drags completed in 13 to 16 fathoms off Campeche during July, 1951, but they are not comparable with the February data because a chain was used instead of a lead line.

I have followed Abbott (1954) in assigning names to most of the molluscan species. As a result of the renewed interest in molluscan systematics there have been numerous name changes and different interpretations of the number of species in some of the more common genera. This is particularly bewildering to the ecologist because often these changes are made without giving adequate synonymies. All field identifications were made by me. If a species was not known when encountered in the field, it was given a name or number and brought into the laboratory for identification. All species reported in this paper are represented by at least one specimen in the collection of the Institute of Marine Science.

Gastropoda

Calyptraeidae

Crucibulum sp.

Cup and saucer limpets were common in 6 to 10 fathoms of water on Campeche Bank during February, 1951. Several additional specimens were taken in 13 to 16 fathoms off Campeche, Mexico during July.

Crepidula spp.

Slipper limpets attach themselves to larger snails and pelecypods and are, therefore, caught in considerable numbers in shrimp trawls. Three species, *Crepidula fornicata*, *Crepidula plana* and *Crepidula aculeata*, were identified in 6 to 10 fathoms of water on Campeche Bank. *Crepidula plana* commonly attaches itself inside the apertures of snail shells, and it was noted as particularly abundant in large shells containing the red hermit crab, *Petrochirus bahamensis*. It was the only species noted in 16 fathoms off Campeche during July. *Crepidula aculeata* was much more abundant than *C. fornicata* in 6 to 10 fathoms during February.

Strombidae

Strombus alatus Gmelin

Fighting conchs occur in great abundance on Campeche Bank, and they are one of most characteristic mollusks on the pink shrimp grounds. Fighting conchs occur in the "shell piles" or "shell ridges", of the shrimp fishermen, and they are not uniformly scattered over the shrimping ground. This species is widely distributed and locally abundant in the western Gulf. Hildebrand (1954) reported dead specimens from Grand Isle, Louisiana, many live specimens in 11 fathoms off Freeport, Texas and fishermen reported it common off Port Isabel, Texas. However, shells rarely wash ashore, and the only place in the western Gulf that I have found them abundant on the shore is on the beach at Boca Chachalaca and Ruinas de Villa Rica near Vera Cruz. Old shells are not uncommon on the beach in Cameron and Vermilion Parish, Louisiana. I recorded this species in 35 drags out of 53 completed on the Campeche Bank during February, 1951, and only in 7 to 8 fathoms off Morros Point was this species absent or very rare in trawl catches. Only a few specimens of this conch were taken in 15 to 16 fathoms off Campeche during July. Therefore, on the basis of limited trawling in deeper water it seems that this species is most abundant in depths of 6 to 13 fathoms on Campeche pink shrimp ground.

Strombus costatus Gmelin

Only a single milk conch was caught in trawls. It was taken in 13 fathoms off Campeche, Mexico on July 28, 1951. I have seen other specimens that were taken on Campeche banks in the collections of Texas fishermen. There is one specimen in a private collection at Port Aransas that was taken alive near the lighthouse on Harbor Island near Port Aransas, Texas. It is unlikely that this species could survive the long trip across the Gulf from the Campeche banks. The large helmet conchs, *Cassis madagascariensis*, failed to survive a three-day trip across the Gulf during February, 1951.

Naticidae

Natica canrena Linné

According to Abbott (1954) this species is common in the West Indies. This species was not common in shrimp trawls. I saw only three snails taken during February from 6 to 10 fathoms.

Cassididae

Phalium granulatum Born

Scotch bonnets were recorded in only four drags on the pink shrimp grounds, and they were not taken in water deeper than 10 fathoms. Presumably this species is more common inshore, as is the case in the northern Gulf (Hildebrand, 1954).

Cassis madagascariensis Lamarck

When the Texas shrimp fishermen extended their shrimping grounds to Campeche Bank during 1950, they were introduced to a new fauna. Among the animals which impressed them most were the emperor conchs. This species together with *Xancus angulatus* and *Pleuroploca gigantea,* often occurred in such abundance that trawling with a heavily leaded foot rope was impractical. I recorded this species in only nine drags completed in 10 to 16 fathoms on Campeche Bank. However, it is reported to be particularly numerous in one small area of the shrimping grounds (see Fig. 1).

Presumably this is the species of mollusk most seriously affected by the shrimp fishermen. It now appears in nearly all curio shops on the Gulf coast and shrimp fishermen have even suggested that the trawlable bottom on Campeche Bank could be increased or improved by dumping large conchs in deep water instead of throwing them back after the completion of a drag. Such a policy has not been carried out by the fishermen, and it is doubtful if it would be practicable, even if desirable, because of the small amount of deck space on the trawlers, and the length of time that they trawl in shallow water.

Cymatiidae

Cymatium sp.

Only a single specimen of this genus was noted in trawl catches from 6–10 fathoms.

Distorsio clathrata Lamarck

Several specimens were taken in ten fathoms during February, 1951. Five additional snails were noted in a single drag in 15–16 fathoms off Campeche during July, 1951. This species is widely distributed on the shrimping grounds in the western Gulf of Mexico (Hildebrand, 1954).

Ficidae

Ficus communis Röding

The fig shell was common in ten fathoms between Campeche and Champoton, Mexico. Usually only a few shells were trawled but in some drags it was very abundant. No fig shells were found at 13 to 16 fathoms off Campeche during July, 1951. Fig shells occur along the west coast of Florida, and I have found them common on the beach a few miles north of Port St. Joe, Florida. Clench (1942) reported the fig shell from Texas, but Pulley (1952) dismisses this record with the comment that they were probably landed by shrimp fishermen from out-of-state waters. Whatever the province of these shells labeled Texas, it is improbable that they originated from shrimp fishermen, because they were collected before 1942 well before the shrimp fleet operated outside of territorial waters. It is probable that this species will be found offshore in the Port Isabel area.

Muricidae

Murex fulvescens Sowerby

The distribution of this species in the western Gulf has been previously discussed by Hildebrand (1954). Only a single specimen was taken in 15 to 16 fathoms off Campeche.

Murex pomum Gmelin

The apple murex was much commoner in the trynet than in the big net. However, it was frequently abundant in depths of 6 to 10 fathoms off Campeche.

Murex florifer Reeve

Two specimens of *florifer* in the collection were taken at depths of 6 to 10 fathoms. This species ranges from southern Florida to the West Indies (Abbott, 1954).

Melongenidae

Busycon coarctatum Sowerby

This is the common species of *Busycon* on Campeche Bank and it is apparently unknown from elsewhere in the Gulf. It was one of the most abundant species in 6 to 10 fathoms on Campeche Bank, but only a single dead shell was recorded in 13 to 16 fathoms off Campeche.

Busycon contrarium Conrad

Apparently this conch is rare on Campeche Bank, at least on the shrimping ground. There are no specimens in my collection, but two were recorded in 13 to 14 fathoms off Campeche.

Busycon perversum Linné

There is a single specimen of this species in my collection from Campeche Bank. It was taken in depths of 6 to 10 fathoms. Hildebrand (1954) stated that this species was widely distributed in the western Gulf.

Busycon spiratum Lamarck

The pear conch is better known as *B. pyrum.* It was not common on Campeche Bank. Pear conchs were listed from 6 drags in 10 fathoms during February, 1951 and sixteen pear conchs were taken in 13 to 16 fathoms off Campeche during July.

Fasciolariidae

Fasciolaria tulipa Linné

Tulip shells were very common on Campeche Bank and they were recorded in 25 of the 53 drags completed during February. Less than 12 shells were taken in 13 to 16 fathoms during August. Tulip shells were one of the dominant mollusks in the trawl hauls. Although Pulley (1952) reports this species from Texas, it is presumably quite rare.

Fasciolaria hunteria Perry

The banded tulip shell was formerly known as *F. distans.* The Yucatan representative of this species has been described as a separate subspecies, *F. hunteria branhamae* Rehder and Abbott.

Pleuroploca gigantea Kiener

The giant horse conch is very abundant on Campeche Bank and it was recorded in 26 drags completed in 6 to 10 fathoms. Certainly the horse conch is one of the dominant species on the shrimp grounds. On the Texas coast, horse conchs are not uncommon in Indian middens (Campbell, 1952), and old shells are not uncommon in the alluvial bluff at Punta Piedras, Tamaulipas on the shore of Laguna Madre. Live specimens may still occur in this laguna as I found a shell in the pass at Boca Jesus Maria that appeared to be fresh. Hildebrand (1954) reported only five small shells from the brown shrimp grounds.

Fusinus couei Petit

Coue's spindle shell is not uncommon on Campeche Bank, but only a few specimens are retained by the shrimp trawl. Scattered shells were taken in 6 to 10 fathoms during February and I did not record this species in 13 to 16 fathoms during July, 1951.

Xancidae

Xancus angulatus Solander

The West Indian chank is one of the most characteristic and abundant mollusks captured in shrimp trawls on the pink shrimp grounds off Campeche, Mexico. Chanks were found in the majority of drags and in a few drags it was excessively abundant in depths of six to sixteen fathoms. According to Abbott (1954) the chank is a West Indian species ranging northward to Campeche and Key West. Apparently this species is unknown from the Tortugas pink shrimp grounds. In the western Gulf, I have found live chanks only off Campeche, but it may occur as far north as Cabo Rojo. At least subfossil chanks are not uncommon in Laguna de Tamiahua on the shores of Isleton de Burro. However, I have never seen a living chank in the Laguna and it is doubtful if they would survive in such a low salinity area.

Olividae

Oliva sayana Ravenel

Apparently this species has not been previously recorded from so far south in Mexico. I obtained a single live snail in a trynet at eight fathoms off the coast of Campeche. A few more dead shells were taken in the trynet. On the Texas coast this species is common along the beach in very shallow water.

Volutidae

Scaphella junonia Shaw

This species is highly prized by shell collectors and curio dealers on the Gulf coast. Shrimp fishermen, particularly Florida fishermen, save every specimen caught. Twelve snails were taken from six to ten fathoms during February and I took none in 13 to 16 fathoms off Campeche during July. This species occurs off the coast of Alabama, but it has not been reported from the Texas coast. Specimens from the white shell sand at Campeche have a white background and have been described as a different subspecies from that off Alabama. Alabama shells have a cream background. Further study is needed before it can be determined if the two subspecies are indeed worthy of recognition, or are merely related to different bottom types.

Cancellaria reticulata Linné

The common nutmeg shell is too small to be taken in the big trawl except accidentally. Several were recorded in 6 to 10 fathoms off Campeche.

Cancellariidae

Conidae

Conus spurius atlanticus Clench

This attractive cone shell is not uncommon on the Campeche Bank. However, only a few are retained by the large shrimp trawl and it was recorded in four drags made in 10 to 16 fathoms off Campeche. This species has not been recorded from the northwestern Gulf.

Pelecypoda

At best the otter trawl is a very poor clam dredge and it gives a very limited and biased sample of the bivalve fauna. Recent improvements of the otter trawl such as the addition of a "jumper chain" have almost eliminated the capture of bivalves except when a shell ridge is crossed. A jumper chain was used exclusively on the "Texas Clipper" and I saw only a few isolated valves or pelecypods such as *Chama* and *Ostrea* that attach themselves to large objects on the bottom. More bivalves are retained by the smaller meshes of the trynet, but such catches are not recorded except to note species not occurring in the large trawl.

Arcidae

Arca zebra Swainson

Shells of this arcid were widely distributed in depths of 6 to 10 fathoms of Campeche during February. Pulley (1952) reports this species from coral reefs off Galveston and beach shells at Port Isabel, Texas. This species needs attachment surfaces and apparently it is common only on shell ridges and around coral reefs. On December 31, 1953 I found large numbers of the zebra arcid in the beach drift at Boca Chachalaca near Vera Cruz.

Anadara lienosa Say

The cutribbed arcid is the largest arcid in the western Gulf. Isolated valves and occasionally hinged valves were found in the trawls in depths of 6 to 10 fathoms off Campeche, where this species is apparently quite common. I have seen fresh empty valves along the Mexican coast as far north as Boca Jesus Maria, but according to Pulley *(op. cit.)* only worn valves are known from the Texas beaches.

Mytilidae

Volsella americana Leach

A single tulip mussel was taken in 15 to 16 fathoms off Campeche on July 27, 1951. This species, judging from beach drift, is widely distributed in the western Gulf, although its fragile shell is usually damaged when found on Texas beaches.

Pteriidae

Pteria colymbus Röding

Two winged oysters were caught in 13 fathoms west of Campeche on July 28, 1951. This species is widely distributed in the western Gulf, where it has a predilection for attaching itself to whip corals.

Pinnidae

Atrina serrata Sowerby

Only dead shells heavily encrusted with bryozoans and other organisms were seen. Possibly the live pen shells bury themselves so deeply that very few live shells are torn loose by otter trawls.

Pectinidae

Aequipecten irradians Lamarck

Old and isolated valves were sometimes found in the trynet and large trawl in depths of 6 to 16 fathoms off Campeche. This species will probably be found in the beds of grass, *Thalassia,* that occur inshore of the area trawled.

Ostreidae

Ostrea equestris Say

This little oyster finds abundant surfaces for attachment on the shell bottom off Campeche. Many examples of this species were seen on Campeche Bank, and in all depths trawled during this investigation.

Lucinidae

Anodontia alba Link

I noted a number of valves of the buttercup lucinid in depths of 10 to 16 fathoms off Campeche. This species was formerly known as *Lucina chrysostoma* and dead shells are common on the Texas beaches (Pulley, 1952).

Chamidae

Chama sp.

The jewel box vies with the horse oyster for attachment surfaces on Campeche Bank. This species is very abundant and it occurred in depths of 6 to 16 fathoms, the vertical range fished.

Echinochama cornuta Conrad

This species is widely distributed in the western Gulf of Mexico and it is very abundant in a few localities off Texas (Hildebrand, 1954). I found this species repeatedly in trynet catches in 6–10 fathoms off Campeche and less often in the large trawl. It appears to be an abundant species on the Campeche Bank.

Cardiidae

Laevicardium laevigatum Linné

Isolated valves of the eggshell cockle were noted in the large trawl in two drags completed in 10 fathoms. It was slightly more abundant in trynet catches. One cockle was taken in 15 to 16 fathoms off Campeche on July 27, 1951.

Dinocardium robustum Solander

Four isolated valves were taken in 6 to 10 fathoms off Campeche during February, 1951. This cockle is an abundant species throughout the western Gulf, if beach shells are any indication of the offshore population. Presumably, it is sometimes eaten by coastal inhabitants near Tuxpan, Vera Cruz, where piles of shucked shells are occasionally found on the beach.

Veneridae

Mercenaria campechiensis Gmelin

Old shell was very common in the trynet catches in 6 to 10 fathoms during February, 1951. Usually the shell was very friable due to the activity of boring clams, sponges and other organisms. Live clams were taken several times and empty hinged clams were not uncommon.

Chione cancellata Linné

Old isolated valves were found in a trynet haul in 16 fathoms off Campeche on July 27, 1951.

Chione intapurpurea Conrad

This species was taken in trynet hauls in 6 to 10 fathoms during February.

Chione latilirata Conrad

A single valve of this species was obtained from a trynet haul in 16 fathoms off Campeche, Mexico.

Macrocallista maculata Linné

Fresh valves of this species were noted several times during February in depths of 6 to 10 fathoms. An empty shell was taken in 15 to 16 fathoms off Campeche on February 28, 1951.

Dosinia elegans Conrad

Discus shells were recorded in 8 drags in 6 to 10 fathoms during February. These catches and examples from the trynets indicate that this is an abundant species on Campeche Bank. Pulley (1952) reported dead shells from Padre Island, but apparently this species is uncommon in the northwestern Gulf. I did not take it during a year of investigating the brown shrimp off Texas (Hildebrand, 1954).

Class Cephalopoda

Family Loliginidae

Loligo pealei (LeSueur)

Squids were very rare in trawl catches on Campeche Bank. However, this may be explained in part by the predominance of night trawling. During February in 6 to 10 fathoms and during July in 13 to 16 fathoms squid were caught, but never more abundantly than a few handfuls per drag.

Octopus vulgaris Lamarck

Large broken horse conchs, *Pleuroploca gigantea,* provide ideal refuge for small octopuses and wherever these shells were taken, octopuses were also found. The maximum number taken was 12 in a two hour drag.

Arthropoda

Crustacea

Stomatopoda

Squilla empusa Say

Mantis shrimp seem to thrive on all shrimping grounds in the Gulf of Mexico and according to Perez-Farfante (1954) they are one of the characteristic associates of the pink shrimp off Batabano, Cuba. Mantis shrimp were recorded in over seventy-five per cent of the drags completed during February, and often they were abundant. Mantis shrimp were caught in all seven drags in 13 to 16 fathoms of water during August.

Lysiosquilla scabricauda Lamarck

This large, conspicuous stomatopod is one of the distinctive members of the Campeche fauna. This squillid was not nearly as abundant as *S. empusa,* and they were recorded in eight drags during February in six to ten fathoms.

Decapoda

Crangonidae

Snapping shrimp abounded in all hauls that contained sponges. No records were kept, but according to Pearse (1932) several species may be expected in a single sponge.

Penaeidae

Solenocera atlantidis Burkenroad

One shrimp, 22 mm. long, which was taken in 15 to 16 fathoms west of Campeche, Mexico on February 28, 1951, was identified by Mr. Burkenroad. He took 369 mature shrimp in a single drag in 19 fathoms off Louisiana (Burkenroad, 1939), and apparently this species has not been recorded since.

Penaeus setiferus (Linnaeus)

Off the coast and in the bays of Louisiana the largest fishery for white shrimp exists. Young shrimp thrive in protected bays with water of low salinity and the adults are fished in great quantities on the offshore mud bottom. Along the eastern coast of Mexico such conditions are most nearly duplicated off the rainy coast of Tabasco and the southern part of Campeche and the most important fishing grounds for white shrimp in Mexico occurs here (Hildebrand, 1954). White shrimp are absent from the west coast of Florida south of Carrabelle. Mr. Burkenroad examined my specimens from Campeche Bank and identified them as *Penaeus setiferus*. *Penaeus schmitti* is the common white shrimp in Cuba (Perez-Farfante, 1953).

While the adults of the white and pink shrimp prefer mud and shell sand respectively, there is some overlapping of ranges in this area and both species may be caught in a single drag. During January, 1951 the fishermen were shrimping for pink shrimp in 8 fathoms during the night and for white shrimp in 17 fathoms during the day. I took no white shrimp in 6 to 10 fathoms on Campeche during February, not even when we fished for pink shrimp in 6 to 10 fathoms off Punta Morros during the day. However, during the February full moon enormous schools of white shrimp were encountered west of Champoton in 15 to 17 fathoms. The shrimp were so tick that it was possible to trawl only a short time. Shrimp were caught at the rate of 60 to 70 barrels (12 to 14 thousand pounds of whole shrimp) a day and the catch would have been even higher if the crews could have handled more shrimp. This heavy run lasted only a few days, but profitable white shrimp fishing continued for at least two weeks. Apparently this offshore concentration is analogous to the winter concentration off Louisiana which existed before the fishing intensity increased. A few white shrimp were taken in 13 fathoms off Campeche during April, 1951 but the number was so small that the crews did not bother to sort them separately. I took 16 white shrimp (14 females/2 males) in 13 fathoms on July 29, 1951. These were all adult shrimp and no others were seen in the remaining six drags completed in depths of 13 to 16 fathoms west of Campeche. However, I did no daytime trawling.

Penaeus aztecus Ives

No brown shrimp were taken during either the February or the July trip to Campeche Bank. However, the ranges of pink and brown shrimp overlap north of Carmen and I took brown shrimp in great numbers on the mud bottom off Obregon. Brown shrimp are lumped with pinks in the Florida shrimp statistics and the term Campeche seems to be quite elastic, so it is difficult to determine the contribution of either species to the Florida landings. Moreover, a single port may receive shrimp from other fishing grounds in the western Gulf of Mexico.

Penaeus duorarum Burkenroad

In the western Gulf it is only on Campeche Bank that pink shrimp flourish in such numbers that they represent the dominant species of shrimp. Due to coral, sponges and algae the fishing ground is very limited, but pink shrimp are known to occur on most of Campeche Bank in depths of less than 28 fathoms. Pink shrimp stray off the banks to the west, and I took a few on the mud bottom off Obregon during August, 1951. Young pink shrimp are found in all parts of the western Gulf except Louisiana, west of the Mississippi River.

My first trip to Campeche Bank was during February, 1951. From February 6 to 16, 1951 we put the large net overboard 53 times. Two drags were entirely lost because of torn nets. However, in the remaining 51 drags we fished for 88 hours and swept 2,940 acres of bottom. The length of these drags varied from fifty minutes to two hours. Three days and nights of fishing time were lost because of rough seas. We caught 22,900 pounds of whole shrimp. The average catch was 260 pounds per hour or 7.8 pounds per acre. For some reason (possibly ground swells) we caught more shrimp during the daytime on February 16 than we did in the same area the preceding and following nights. In fact, our greatest hourly catch (515 pounds) was caught during the daytime. The least amount of shrimp caught during an hour of dragging was 65 pounds.

During July 1951 we completed seven drags in 13 to 16 fathoms west of Campeche. Eighteen hours of night trawling was done between July 27 to 29. The average catch was 180 pounds per hour or 5.4 pounds per acre.

Very few measurements of shrimp were taken. The smallest measured was 68 mm. long, but it is probable that a few smaller shrimp were caught. Some shrimp were discarded as too small, but the number was not great. The count of the shrimp varied from 15–20 to 31–36 in the commercial catch. Small shrimp are difficult to head, and when large catches are being made, they cannot be handled fast enough. No attempt was made to save shrimp smaller than 36 count, and when many small shrimp were caught we tried trawling elsewhere. Almost all shrimp caught were 21–30's (heads on count).

NATURAL HISTORY

Very little information on the natural history of the pink shrimp has accumulated. It appears from the work of Springer (1952) that the vertical bathymetric range of the pink shrimp closely approximates that of the white shrimp, *Penaeus setiferus.* The pink shrimp is very rare at depths greater than 28 fathoms and Springer and Bullis (1954) reported no captures at depths greater than 37 fathoms anywhere in the Gulf of Mexico. The adults of the pink shrimp are concentrated on white shell sand bottom, while the brown shrimp and white shrimp thrive on mud bottom. Pink shrimp, according to fishermen reports, are taken on hard sand bottom off Mississippi and Alabama. No pink shrimp have been reported from Louisiana waters west of the Mississippi and apparently the low salinity and muddy bottom offshore bar the "pinks" from that region.

There is evidence according to Burkenroad (1949) that the young pink shrimp are found predominantly on the shallowest bottoms of the saltiest sounds in North Carolina. Higman (1952) reported a live bait fishery based on this shrimp in Florida Bay and among the Florida keys. This area is characterized by dense beds of *Thalassia* and *Sargassum* and these plants provide cover for the young shrimp. Larger shrimp are caught by channel or lift nets and during the winter months, large catches are sometimes made in nets suspended from bridges spanning the channels between the Keys. De Sylva (1954) reported on a pushnet bait fishery in the Oak Hill-New Smyrna area from April to the first cold weather (usually in December). This area is characterized by large shallow grassy flats, and the majority of the shrimp taken are pink shrimp. The salinities during August were 20 to 22 ‰. On the south Texas coast I have found pink shrimp in the bays throughout the year, but they are most abundant during the spring months. During March and April, a high percentage of the live bait shrimp are this species. According to Gunter (personal communication) pink shrimp are now much more abundant in the Aransas Bay area than formerly when the average salinity of the bay was much lower.

Nearly all my records of small shrimp are from areas of grassy bottom, and the greatest concentrations have been found in Redfish Bay, where the bottom is chiefly covered with *Thalassia*. Pink shrimp have also been taken from the southern part of Laguna Madre on the shallow grass *(Diplanthera)* flats. No large concentrations of adults have been reported even locally off the Texas coast, but small shrimp around 60 count (60 to the pound) are often taken in depths of 0 to 10 fathoms during March to June, but there is no specific fishery for them (Hildebrand, 1954). From the above comments it appears that the young shrimp prefer shallow grassy flats with salinities of 20 ‰ or more, and the adults concentrate offshore on shell or hard sand bottom in water less than 28 fathoms deep.

Trachypeneus constrictus (Stimpson)

Trachypeneus constrictus is a small shrimp; a large female will measure around 90 mm. in length. Very few were captured on Campeche Bank and I found this species in only 19 hauls out of 51 completed during February, 1951. There appears to be no single factor that separates the niches of *T. similis* and *T. constrictus*. *T. similis* is commonly associated with *P. aztecus* on the mud bottom in the western Gulf in depths of 10 to 30 fathoms. However, Burkenroad (1939) found *T. similis* common in Pensacola Bay and *T. constrictus* common in the outside waters off Pensacola and Mobile Bay. He further found that *T. similis* was the most abundant species west of 88° 10′ in the Gulf. On the basis of these records, he suggests that *T. constrictus* is a creature primarily of sandy bottoms and *T. similis* of muddy bottoms. My work off the coast of Texas (Hildebrand, 1954) and off Campeche indicated that the distribution of the species would correlate better with bottom type than salinity and temperature relationships. No trachypeneid shrimp were taken in 13 to 16 fathoms during July, 1951.

Sicyonia brevirostris (Stimpson)

Next to the pink shrimp, this rock shrimp was the most abundant crustacean on Campeche Bank. Rock shrimp were found in every drag completed there. It was much more abundant in 6 to 10 fathoms during February than in 13 to 16 fathoms. At no time was this species found in commercial quantities, although it is probable that several barrels were caught during February. Moreover, there was no indication that this species was more abundant in daytime rather than nighttime drags.

Sicyonia dorsalis (Kingsley)

I found this species to be the most common sicyonid on the brown shrimp ground in the western Gulf of Mexico (Hildebrand, 1954). *S. dorsalis* was not taken in depths of

6 to 10 fathoms during February and it was rare in depths of 13 to 16 fathoms west of Campeche during July. I took 4 specimens in the big net and two in the trynet during July. Although small specimens are sometimes taken in the mouths of the bays in Texas, particularly in the ship channels, the majority are taken in depths greater than 10 fathoms (Hildebrand, *op. cit.*).

Porcellanidae

Porcellana sayana (Leach)

This species was very abundant on Campeche Bank, but no data were kept on its abundance. Other porcellanids were seen, and *Petrolisthes* was not uncommon in drags containing sponges.

Paguridae

Petrochirus bahamensis (Herbst)

Large gastroped shells abounded on Campeche Bank and this species was likewise very abundant. No numerical records were kept, but it was taken in nearly every drag completed on Campeche Bank.

Majidae

Libinia dubia Milne-Edwards

I have never found spider crabs abundant in trawl catches anywhere in the western Gulf and Campeche Bank was no exception. Usually only one or two crabs are taken during an hour's drag. Spider crabs were recorded in ten drags on Campeche Bank, and two was the maximum number recorded per drag.

Podochela riisei Stimpson

Only a single crab was taken in a trynet in 13 fathoms of water off Campeche on July 28, 1951. Small long-legged spider crabs would be crushed by fish and other organisms in the large trawl. Consequently they are rarely found.

Parthenopidae

Parthenope serrata (Milne-Edwards)

One specimen was taken in 15 to 16 fathoms of water off Campeche, Mexico on July 28, 1951. Parthenopid crabs are rarely caught in large otter trawls.

Portunidae

Portunus spp.

I obtained both *Portunus gibbesi* and *Portunus spinimanus* on Campeche Bank, but I found on examining preserved specimens that I had not always properly separated the two species in the field. *Portunus* was taken in every drag completed on Campeche Bank, and it greatly exceeded any other species in abundance. While both *Portunus gibbesii* and *Portunus spinimanus* were often taken in the same drag. *Portunus spini-*

manus was the most abundant in the trawl catches. Both species appear to be rare on the Texas coast (Gunter, 1950, Hildebrand, 1954) and the niche which they occupy on the pink shrimp ground seems to be filled by *Callinectes danae* on the brown shrimp grounds of Texas.

Callinectes danae Smith

The Gulf blue crab was replaced on Campeche Bank proper by species of *Portunus*, and it was only on the southern end of the bank from Punta Morros to a few miles south of Champoton that I encountered this species. I recorded the crab in 16 drags completed in depths of 8 to 10 fathoms, but it was never abundant. Crabs caught on the white shell sand were a pastel blue, while those caught on the mud bottom off Obregon to the west are a dark olive. This species apparently thrives on mud bottoms.

Xanthidae

Xanthid crabs were extremely abundant in all trawl hauls that contained sponges. They were not recorded by species.

Leucosiidae

Persephona punctata (Linnaeus)

One specimen was taken in a trynet in 8 fathoms off Punta Morros on February 16, 1951.

Dromiidae

Dromidia antillensis Stimpson

According to Rathbun (1937) this species ranges from North Carolina to Brazil and from the shore to 170 fathoms. It has been reported from Aransas Pass (Rathbun, 1937) but it is very rare. I have taken only one specimen in Aransas Pass and I have not seen it elsewhere along the Texas coast during three years of work. Wherever ascidians are caught on Campeche Bank, this little crab is certain to be found with one on its back. It was taken in depths of 6 to 16 fathoms, the depth range trawled on Campeche Bank.

Calappidae

Calappa flammea Herbst

Calappid crabs are rarely absent from any trawl hauls in the offshore waters of the Gulf. They were taken in all but four drags completed in depths of 6 to 16 fathoms on Campeche Bank. More than five are rarely taken per hour of trawling. This absence of aggregations of *C. flammea* agrees with the distribution of *Calappa springeri*, which occurs on the adjacent mud bottom off Obregon and in the northwestern Gulf.

Hepatus epheliticus (Linnaeus)

Calico crabs, according to Rathbun (1937), range from the Chesapeake Bay to Texas. My records extend the range to the Gulf of Campeche, where it appears to be common and as abundant as it is in Texas waters. I recorded it in 43 drags completed in depths of 6 to 16 fathoms on Campeche Bank. The largest number recorded in a single drag was 10. One female with a purple sponge was found in 15 to 16 fathoms of water on July 28, 1951.

Echinodermata

Asteroidea

Astropectenidae

Astropecten articulatus valencienni Müller and Troschel

This starfish was caught in depths of 6 to 10 fathoms during February. Only a few specimens were saved. One starfish thought to belong to this species was taken in 13 fathoms off Campeche on July 29, 1951.

Luidiidae

Luidia clathrata (Say)

This starfish is widely distributed in the Gulf of Mexico. It has a tendency to bury itself in the sand and is never captured in any numbers by the shrimp trawlers. Several were seen during February in depths of 6 to 10 fathoms.

Oreasteridae

Oreaster reticulatus (Linnaeus)

This is a very common species in the West Indies and it appears in curio shops throughout the United States. As many as 12 per hour of trawling were taken in 7 to 16 fathoms off Campeche. This species is apparently confined to shell bottom and it is unknown from the northwestern Gulf.

Echinasteridae

Echinaster echinophorus (Lamarck)

Whenever I found loggerhead sponges in the large trawl, I also encountered this small starfish. It was not recorded on the shell sand bottom off Punta Morros. This species has also been recorded from the Texas coast (Hildebrand, 1954). *Echinaster spinulosus* from off Alabama and *Echinaster sentus* from Tortugas are closely related species, if not synonyms of this species.

Ophiuroidea

Brittle or serpent stars were abundant in sponges on Campeche Bank, but I did not record them by species.

Echinoidea

Arbaciidae

Arbacia punctulata (Lamarck)

This species is very common around the jetties at Port Aransas and Brazos Santiago, Texas, but sea urchins are rarely captured in trawls nor are they seen on sandy bottom in Texas waters. Five spiny sea urchins were taken in one drag in 7 fathoms of water. This was the maximum number taken during the investigation. This and the following species were taken in 7 fathoms off Punta Morros.

Lytechinus variegatus (Leske)

Several sea urchins were taken in 7 fathoms off Punta Morros on a shell sand bottom. This species appears to be more common than *Arbacia* in that area.

Clypeastridae

Clypeaster subdepressus (Gray)

A few specimens were taken in 7 to 10 fathoms off Punta Morros. This species was more common in trawl hauls than *Encope michelini,* which was on several occasions captured in the same haul.

Encope michelini Agassiz

Several specimens of this urchin were taken in 7 fathoms off Punta Morros. Either no large beds of this species exist in most of the area trawled, or it escapes the trawl because of its burrowing habits. A large number was taken in a trynet on February 15, 1951 in 8 fathoms.

Plagiobrissus grandis (Gmelin)

A single specimen of the cake urchin was taken in 7 fathoms off Punta Morros on February 15, 1951. The bottom was a white shell sand.

Holothuroidea

Stichopidae

Asticopus multifidus Sluiter

One of the characteristic organisms of the pink shrimp ground is this large stinking sea cucumber. It was common in depths of 6 to 16 fathoms off Campeche, although it was rarely captured at a rate of more than 15 per hour of trawling. Previously, this species has been only known from Tortugas Islands.

Cucumariidae

Thyone briareus (LeSueur)

One specimen of this holothurian from 6 to 10 fathoms on Campeche Bank was identified by Dr. E. Deichman. Small holothurians are rare in trawl catches and my few catches are hardly an indication of the rarity or the abundance of this species on Campeche Bank.

Chordata

Ascidiacea

Ascidians often appeared in the trawls in considerable numbers, and although one black species was very conspicuous, they were never the dominant organism in the trawl catches. Ascidians were not identified in the field and they were recorded only by the group name or by distinctive characteristics. I am indebted to Mr. Donald Moore for the identification of the Campeche collection. At least seven species are represented in the collection. *Eudistoma capsulatum* (Van Name) is a blackish species, at least on Campeche Bank, and its color contrasted strongly with the white shell sand bottom, but not with the loggerhead sponges with which it commonly occurred. *Eudistoma* sp., a capitate form, was abundant and widely distributed on the shrimping grounds. *Amaroucium stellatum* Verrill was carried by the little dromid crab, *Dromidia antillensis,* as a protective shield. A species of *Didemium* is sometimes used by this crab on the Texas coast. A sea onion, only *Styela plicata* in the collection, was common nearly everywhere that trawling was done on the banks. *Microcosmus exasperatus* is present in the collection, but it was not commonly taken.

Gnathostomata

Pisces

Chondrichthyes

Selachii

Carcharhinidae

Carcharhinus acronotus (Poey)

A single requiem shark, 542 mm. long, was taken in 13 fathoms west of Campeche on July 28, 1951. Springer (1950) found that this species prefers coral mud. Therefore, it should be abundant on Campeche Bank.

Carcharhinus obscurus (LeSueur)

No ridgebacked requiem sharks were taken in the trawl, and most of the sharks belonging to this group appear to be pelagic. One small shark, 3½ ft. in length, was taken on a hook and line in 13 fathoms of water west of Campeche on July 28, 1951.

Sphyrnidae

Sphyrna tiburo (Linnaeus)

There were no reports of shark damage to gear on Campeche Bank during February, 1951, and sharks were, indeed, rare in the trawl catches of the "San Jacinton." Nineteen shovel-nosed sharks comprised the catch of sharks. Eight sharks were taken in one two-hour drag in 10 fathoms off Campeche and the remaining eleven sharks were distributed among seven other drags completed in depths of 7 to 10 fathoms. No shovel-nosed sharks were taken in 13 to 16 fathoms during July. Presumably, this little shark is equally at home on the shell sand of Campeche Bank and the mud bottoms of Texas bays.

Sphyrna tudes (Cuvier)

A small hammerhead shark, 600 mm. long, was captured at 13 fathoms west of Campeche on July 28, 1951. This species was identified on the basis of an indentation in the middle of the front margin of the "hammer," serrate teeth and the short posterior lobe of the second dorsal fin.

Batoidea

Rhinobatidae

Rhinobatus lentiginosus (Garman)

Twenty-six guitarfish were caught during February in 6 to 10 fathoms of water. They were not numerous and the maximum number taken in a single drag was six fish. Nine additional guitarfish were taken in 13-16 fathoms during July.

The spotted color of the Campeche specimens and uniform brown color of Texas specimens has been previously discussed by Hildebrand (1954). Bigelow and Schroeder (1954) found one specimen among 13 guitarfish from Texas with a faint indication of spotting, and the remainder of their specimens from Florida, Campeche and the Atlantic coast of the United States were spotted. The range of the uniform brown guitarfish has not been delineated in the northern Gulf, but I saw one seined on the beach at Tecolutla, Vera Cruz during December, 1954.

Torpedinidae

Narcine brasiliensis (Olfers)

Six torpedo rays were taken in depths of 6 to 10 fathoms during February and this species was not encountered during July in depths of 13 to 16 fathoms. Torpedo rays are predominantly shallow water inhabitants on the northern Gulf coast where they are often taken in beach seines during the summer months (Gunter, 1945). Possibly, the majority of the torpedo rays was distributed inshore of the area trawled on Campeche Bank.

Rajidae

Raja texana Chandler

Although Bigelow and Schroeder (1954) expressed some doubts as to the distinctness of *R. texana* and *R. ocellata,* they maintain the two as separate species. Our specimens correspond most closely with the description of *Raja texana.* From my trawling records and the published records of *Raja texana* and *ocellata* it would seem that skates are rare on the bank. Nineteen specimens were taken in depths of 6 to 10 fathoms during February. In other words, they were taken in thirteen drags or approximately one-fourth of the drags completed, while on the mud bottom of the brown shrimp grounds they were caught in nearly every drag. Only one small specimen was taken in 13 to 16 fathoms during July on the bank, while on the neighboring mud bottom off Obregon they were common (Hildebrand, 1954).

Dasyatidae

Dasyatis americana Hildebrand and Schroeder

Two stingrays were caught on Campeche Bank during February in 6 to 10 fathoms. They are characterized by an obtuse rostrum and a small keel instead of a flap on the upper surface of the tail. The color was a very light brown. The largest stingray measured 610 mm.

Gymnuridae

Gymnura micrura (Bloch and Schneider)

Two butterfly rays were caught in depths of 6 to 10 fathoms during February and one was obtained in 13 fathoms off Campeche during July. This species does not seem to be abundant anywhere in the western Gulf (Gunter, 1945; Hildebrand, 1954).

Urolophidae

Urolophus jamaicensis (Cuvier)

Bigelow and Schroeder (1954) state that this species is confined to shoal waters and most recorded captures are from harbors and bays. Only two specimens captured in 8 to 9 fathoms off Punta Morros during February were recorded during this survey.

Osteichthyes

Isospondyli

Albulidae

Albula vulpes (Linnaeus)

A bonefish, 215 mm. in standard length, was captured in 7 fathoms of water off Punta Morros on February 14, 1951. Gunter (1952) has previously reported this species from the Campeche shrimp fishing grounds. Bonefish may be abundant on the shallow water flats off the Yucatan peninsula, and Mather (1951) reported bonefish as very common on the shallow flats in the Gulf of Honduras but he apparently did not find them common on Campeche Bank.

Clupeidae

Sardinella anchovia (Cuvier and Valenciennes)

This active little fish is chiefly pelagic and is, therefore, seldom taken in a shrimp trawl. It was recorded twice in trawls during February, 1951. During July it was slightly more common in trawl catches and it was recorded in four out of seven drags completed. This species has not been recorded from the northwestern Gulf.

Harengula pensacolae (Goode and Bean)

Although Rivas has recorded three species of *Harengula* from the Yucatan region, only *H. pensacolae* is represented in our collection and it is doubtful if either of the other two species were taken on the shrimping grounds. During February the Gulf sardine was taken in 10 drags in depths of 6 to 10 fathoms, but it was marked common in only two drags. No sardines were caught in 13-16 fathoms west of Campeche during July, although it was found in the same depths off Obregon, Mexico a few days later (Hildebrand, 1954).

Gunter (1945) has shown that the Gulf sardine is very common in the shallow waters of the northwestern Gulf from April to November. The winter concentrations of this species have not yet been discovered.

All specimens taken on Campeche Bank were large and thirty-three sardines from 6 fathoms off Punta Morros ranged in length from 140 to 151 mm.

Opisthonema oglinum (LeSueur)

More thread herring were caught in trawls than any other clupeid fish. However, they were recorded in only nine drags. Twenty-five thread herring caught in 6 fathoms off Punta Morros on February 14, 1951 ranged in length from 140 to 160 mm. Undoubtedly trawl catches of pelagic fishes are not a reliable indication of abundance. This species was not taken in 13 to 16 fathoms during July.

Brevoortia gunteri Hildebrand

Eight menhaden were taken in 2 drags in 7 to 8 fathoms west of Punta Morros on February 15, 1951. On the basis of numerous fine scales (over 70), 28 to 29 scutes and shape of the ventral fin these fish were placed in the species *gunteri*. Gunter (1945) found that the postlarval young of this species are common in February and March in Copano Bay and he further presents some evidence that the adults spawn in Copano and Aransas Bays. He thought that the separation of this species and *B. patronus* was in part determined by the predilection of *gunteri* for water of lower salinity than *B. patronus*. However, the discovery of this species off the coast of Tamaulipas and Campeche by the present writer may indicate that this species has a more southern distribution and in the zone of overlap with *B. patronus* it is most common in waters of low salinity. Hildebrand (1948) reported *gunteri* from Brazos Santiago to Grand Isle. Since that date there have been no published reports of the species east of the Mississippi, and presumably it is quite rare in Louisiana waters. *Brevoortia gunteri* is not known to occur in large schools, and I have not seen nor heard of large schools of menhaden in the Gulf, south of the Rio Grande. In the Gulf of Mexico menhaden appear to be most abundant in the area strongly influenced by the Mississippi River. Here, *B. patronus*, the common species, is caught commercially from April to November.

Engraulidae

Anchoa hepsetus (Bonnaterre)

Anchovies escape through the meshes of large otter trawls and they are rarely captured in deep water. I took ten anchovies in eight fathoms southwest of Campeche on February 12, 1951. These anchovies ranged in length from 116 to 118 mm.

Apodes

Muraenidae

Gymnothorax vicinus (Castelnau)

One very pugnacious moray eel was taken in 9 fathoms west of Campeche on February 6, 1951. This species is apparently a common inhabitant of the coral patches and it is rarely taken in shrimp trawls.

Iniomi

Synodontidae

Synodus foetens (Linnaeus)

Lizard or cigarfishes appear to be common in shallow water everywhere in the western Gulf. This species seems to be more common on the mud bottoms off Texas and Tamaulipas than on Campeche Bank. Nevertheless, it was recorded in over 85 per cent of the drags completed during February and in all seven drags completed during July.

Synodus intermedius (Agassiz)

A single lizardfish was recorded in 13 fathoms west of Campeche on July 28, 1951. This species is apparently common in the Florida Keys and around Tortugas where Longley (1941) reported this species from shallow water to 60 fathoms.

Trachinocephalus myops (Forster)

The snakefish is a conspicuous member of the fauna on Campeche Bank even if it is not abundant. Snakefish are unknown in the northwestern Gulf. This species was recorded in only five drags during February, but it was taken in four out of seven drags completed during July in 13 to 16 fathoms. It is apparently most abundant on shell or calcareous bottoms, as I took it in only a single drag off Obregon (Hildebrand, 1954).

Synentognathii

Exocoetidae

Flying fishes are pelagic and they were never taken in trawls. Although they are rarely sighted on the shrimp grounds, several species are not uncommon over the banks. However, flying fishes are commonly sighted when crossing the Gulf from Campeche to Texas ports and often they land on the deck of shrimp trawlers. All specimens reported in this paper were picked up on the deck of the trawlers.

Parexocoetus brachypterus littoralis Breder

Nine flying fish were picked up on the deck of the "San Jacinto" when it was sailing from Arcas Cay to Campeche over depths of 11-27 fathoms on the night of February 6, 1951. These fish ranged in length from 112 to 119 mm. This species was not recognized nor captured elsewhere during the trips across the Gulf.

Exocoetus obtusirostris Günther

A flying fish, 68 mm. in standard length, was found on deck during the night of February 18, 1951. The dead reckoning position of this capture is over Sigsbee Deep in the vicinity of 23° N. and 94° W.

Cypselurus furcatus Mitchill

Three fish were found on the deck of the trawler on February 4, 1951. The dead reckoning position was 23° 50′ N. and 94° 10′ W. These flying fish ranged in size from

112 to 128 mm. in standard length. This species with its banded pectoral fins was commonly sighted on the trip across the Mexican Basin during February, 1951, but none were observed during the July and August crossing.

Cypselurus heterurus (Rafinesque)

Large blue "four winged" flying fish were common over Sigsbee Deep during February, 1951, and they were present but less abundant during the July and August crossing. Two fish, 185 mm. in standard length, respectively, were found on the deck of the "San Jacinto" during the night of February 4–5, 1951. The dead reckoning position was over the Mexican Basin at approximately 23° 50′ N. and 94° 10′ W. Three other fish, 194-213 mm. were captured over Campeche Bank in depths of 27 to 11 fathoms between 20° to 22° N. and 91° to 92° W. on the night of February 6, 1951. No flying fish were seen inside of the ten fathom curve, but I observed this species during April, 1955 between Blanquilla Reef and Cabo Rojo in less than five fathoms on the coast of Vera Cruz. On February 18, 1951, two flying fish were found on deck near the outer edge of Campeche Bank on a direct compass course from Champoton, Mexico, to Aransas Pass, Texas. These fish range in length from 189-218 mm. One more fish was collected over the Mexican Basin on February 18, 1951.

Flying fish were rare during the July trip across the Mexican Basin, and one could watch the surface of the sea for an hour at a time without seeing more than 5 flying fish at any one time. Three fish were obtained by placing a light on the deck at night during the trip across the Gulf during July. No fish were obtained on the return trip during August. These three fish were captured along a compass course from Port Aransas, Texas to Arcas Cay. One fish, 193 mm. in standard length, was picked up around the 100 fathom curve off Port Aransas on July 25, 1951; another was taken over Sigsbee Deep; and the third fish was captured on the seaward edge of Campeche Bank.

Although all flying fish found on deck were large, small flying fish about the size of monarch butterflies were very common during February, 1951 and they were particularly abundant over the Mexican Basin on February 18, 1951. Possibly they belonged to this species, but none were captured to verify this supposition.

Heterosomata

Bothidae

Ancylopsetta quadrocellata Gill

Only a few, usually less than five, ocellated flounders were caught per hour of trawling. Ocellated flounders were caught in 24 of the 53 drags attempted on Campeche Bank during February, 1951. Seven more flounders were caught in 13 to 16 fathoms during July. One female, 270 mm. long, had spent ovaries, and it was captured on February 12, 1951 in 8 fathoms.

Syacium gunteri Ginsburg

Syacium gunteri and *Syacium papillosum* are easily separated in the field once one becomes familiar with the two species. *Syacium gunteri* is a deeper bodied fish and it does not reach as large a size as *S. papillosum*. *S. gunteri* is not nearly as common as

S. papillosum on the calcareous substratum, but on the mud bottomed brown shrimp, *P. aztecus*, grounds *S. gunteri* is one of the most abundant species of fishes (Hildebrand, 1954). This species was often taken in the same drag with *S. papillosum* in depths of 6 to 10 fathoms during February but it was not as common as the latter. During July few flounders were taken in 13 to 16 fathoms off Campeche, but this species was slightly more abundant than *S. papillosum.*

Syacium papillosum (Linnaeus)

This flounder was taken in nearly every drag on Campeche Bank both during February and July. It was never abundant, but it is possible that gear selection (jumper chain and lightly leaded foot rope) subtracted from the total catch. According to Longley (1941) this species is predominantly an Antillean species and off Tortugas he found this species common on a gray mud bottom in depths of 40 to 60 fathoms.

Cyclopsetta chittendeni Bean

Only two Mexican flounders were taken in trawls on Campeche Bank during February, 1951. Hildebrand (1954) has shown that this species is not common inside 10 fathoms on the Texas coast, so its rarity inside 10 fathoms on Campeche Bank was not unexpected. As many as 10 flounders per hour of trawling were captured in 13 to 16 fathoms west of Campeche, Mexico during July, 1951.

Cyclopsetta fimbriata (Goode and Bean)

Longley (1941) found this species in depths of 10 to 65 fathoms south of Tortugas. It is very rare on the shrimping grounds of Campeche Bank and only two specimens were taken in 6 to 9 fathoms of water during February.

Citharichthys macrops Dresel

C. macrops was one of the commonest flatfishes on Campeche Bank. Surprisingly, Longley (1941) records only two specimens from Tortugas. The color pattern of our Campeche specimens is as Longley described it, a contrasting one of dark spots scattered on a white background. Flounders from the mud bottoms of the northern Gulf have a dark brown background. It was taken in 6 drags during February in 6 to 10 fathoms and in 6 out of 7 drags completed during July in 13-16 fathoms.

Etropus crossotus Jordan and Gilbert

Small mouthed flounders were taken in nearly every drag completed on Campeche Bank. It was more abundant in 6 to 10 fathoms during February than in 13-16 fathoms during July. In a few drags it was the most abundant flatfish and among the flatfishes only *Bothus ocellatus* exceeded this species in abundance in the 6 to 10 fathom area off Campeche.

Longley and Hildebrand (1941) report only *Etropus rimosus* Goode and Bean from Tortugas. My specimens were identified as *Etropus crossotus* by the gill raker count (6 to 7 on lower half) and the absence of scales on the snout. The whitish color of the Campeche fish contrasts strongly with the deep brown of Texas specimens.

Bothus ocellatus (Agassiz)

Occasionally, this species ranges as far north as New York, but it is apparently rare in the northeastern Gulf and it is unknown in the northwestern Gulf. On Campeche Bank this little flounder was the commonest flatfish in depths of 6 to 10 fathoms during February. It was also common in 13 to 16 fathoms off Campeche during July.

Achiridae

Gymnachirus texae Gunter

Only five specimens of this little zebra sole were taken in six to ten fathoms during February, 1951. It appears to be much more common in depths of 14 to 25 fathoms off the Texas coast on mud bottom (Hildebrand, 1954) than on calcareous sediments.

Gymnachirus williamsoni Gunter

More information is needed on the taxonomic status of the two nominal species of naked soles from the Gulf of Mexico. Although I did not find meristic differences between the two species, *williamsoni* reaches a larger size and the dark bands are much wider than in *texae.* One fish 122 mm. long was taken in 10 fathoms off Campeche, Mexico on February 10, 1951. The other specimen of *williamsoni* was taken in 15-16 fathoms off Campeche on July 27, 1951. This species seems to prefer calcareous sands, and it has been reported from Tortugas, Pensacola and Campeche Bank. It has not been taken in Texas.

Achirus lineatus (Linnaeus)

The lined sole was a common flatfish in 6 to 10 fathoms off Campeche during February, but none were taken in 13 to 16 fathoms during July. I recorded this species in 32 out of 53 drags attempted during February.

Cynoglossidae

When this study was undertaken the tongue soles had not been revised by Ginsburg and my data are all grouped. Tongue soles were recorded in 25 drags completed in 6 to 10 fathoms and four drags in 13 to 16 fathoms. The following notes on the individual species are based on the preserved collection of the Institute of Marine Science.

Symphurus plagiusa (Linnaeus)

Seventeen specimens from 6 to 10 fathoms are in the collection. This species was particularly common in 7 to 8 fathoms off Punta Morros. Additional specimens (six) were taken in 13 to 16 fathoms west of Campeche during July. In some specimens there is a black blotch on the opercle, but the background color is much lighter than in Texas specimens.

Symphurus civitatum Ginsburg

There are only three specimens in the collection and they were taken in 13 to 16 fathoms off Campeche during July. In the northern Gulf this species usually occurs offshore in deeper water than the closely related *plagiusa* (Ginsburg, 1952; Hildebrand 1954).

Symphurus diomedianus (Goode and Bean)

Four specimens of this species were taken in 13 to 16 fathoms west of Campeche during July. This species seems to prefer shell sand and coral.

Symphurus urospilus Ginsburg

This conspicuously banded species with a black caudal spot was described by Ginsburg from Savannah, Georgia, in 12 fathoms and off Pepperfish Key, Florida in 19.5 fathoms. Apparently this tongue sole is a shallow water species that prefers coral or shell sand bottoms. This species is unknown in the northwestern Gulf. I took 3 specimens in 7½ fathoms off Punta Morros on February 16, 1951 and 9 specimens in 13 to 16 fathoms west of Campeche during July.

Lophobranchii

Syngnathidae

Syngnathus louisianae Günther

A single male pipefish, 305 mm. in standard length, was taken in 8 fathoms off Punta Morros on February 15, 1951. It carried eggs in its brood pouch.

Hippocampus hudsonius DeKay

Seahorses are rarely captured in shrimp trawls in the northwestern Gulf, and probably the few that are captured come from the floating sargasso weed. However, on Campeche Bank they are very common and I recorded them from 15 drags completed in 6 to 10 fathoms during February, 1951. Cliff Goette informed me that during the preceding month, they had trawled into a seahorse "corral" and caught many seahorses. This "corral" was in a grassy area in 5 to 6 fathoms, but whether by "grass" an algae or a spermatophyte, such as *Thalassia*, is meant is unknown. *Thalassia* was sometimes observed in the shrimp trawl, but I do not know if it was actually growing in depths of 36 to 60 feet or if it was merely drift. Many of the seahorses had eggs or young in their brood pouches. They varied greatly in color, the common colors being white, orange and a dark olive green.

Percomorphii

Sphyraenidae

Sphyraena guachancho Cuvier and Valenciennes

Although the great barracuda is widely distributed around reefs and snapper lumps in the Gulf of Mexico, it seems that only the small West Indian barracuda is caught in shrimp trawls. Seven barracuda were caught in depths of 6 to 10 fathoms during February. Although none were taken in 13 to 16 fathoms during July on Campeche Bank, this species was not rare on the mud bottom off Obregon.

Polynemidae

Polydactylus octonemus (Girard)

Threadfins were recorded in 34 out of 53 drags during February. Usually only a few were taken but in several drags it was noted as common. Threadfins were taken in only three drags during July in 13 to 16 fathoms, and the maximum recorded in a single drag was 20 fish.

Thunidae

Sarda sarda (Bloch)

The bonita is a very common sports fish in the northwestern Gulf, but I have never seen a trawl-caught specimen in those waters. Six fish were taken in a single trawl haul in 16 fathoms west of Campeche on July 27, 1951. Rivas (1951), without examining any specimens from the western Gulf, concluded that the common species in that region should be *orientalis.* All specimens that I have examined key out readily to *Sarda sarda.*

Cybiidae

Scomberomorus maculatus (Mitchill)

Four Spanish mackerel were taken in 6 to 10 fathoms during February. This pelagic fish is rarely taken in shrimp trawls.

Stromateidae

Poronotus triacanthus (Peck)

This very abundant fish in the northwestern Gulf (Hildebrand, 1954) was very rare on Campeche Bank. A single specimen was taken in 15–16 fathoms during July. Longley (1941) did not list this species from the Tortugas Islands.

Carangidae

Decapterus punctatus Agassiz

The round scad was taken in 12 drags completed in 6 to 10 fathoms on Campeche Bank during February. Only two specimens were taken in depths of 13 to 16 fathoms during July. Longley (1941) reported this species from Tortugas in depths of 11 to 22 fathoms.

Selar crumenophthalmus (Bloch)

A single specimen, 182 mm. in standard length, was taken in 13 fathoms west of Campeche on July 28, 1951.

Caranx crysos (Mitchill)

The hardtail jack was recorded in only two drags in 6 to 10 fathoms during February. Two specimens in the collection measure 155 and 165 mm. in standard length, respectively.

Caranx hippos (Linnaeus)

The common jackfish is widely distributed throughout the Gulf, but only small fish are taken in trawls. This species was recorded in eight drags in depths of 6 to 10 fathoms during February.

Caranx latus Agassiz

A single specimen, 185 mm. long, was taken in 6 to 10 fathoms during February.

Caranx ruber (Bloch)

Next to *Caranx hippos,* this was the most common jackfish in the shrimp trawls. It was recorded from seven drags in depths of 6 to 10 fathoms during February.

Chloroscombrus chrysurus (Linnaeus)

While other carangids are more or less pelagic and are rarely caught in trawls, this species is often extremely abundant. Bumpers were especially abundant in the daytime drags in 6 to 8 fathoms off Punta Morros during February. As Broad (1950) and Hildebrand (1954) have noted, the drags in the middle of the night contain fewer fishes than do the early evening and morning drags, and the daylight drags contain the most fish. Bumpers were recorded in 36 drags in 6 to 10 fathoms during February and in three of these drags it was listed as the most abundant fish. This species was also abundant in 13 to 16 fathoms during July.

Vomer setapinnis (Mitchill)

Moonfish were rare on Campeche Bank and it was recorded in only six drags during February. It was slightly more abundant in 13 to 16 fathoms during July, when it was recorded in 5 out of 7 drags.

Seriola dumerili (Risso)

A small amberjack, 149 mm. in standard length, was taken in 10 fathoms on February 10, 1951.

Trachinotus carolinus (Linnaeus)

A single pompano was taken in nine fathoms off Punta Morros on February 16, 1951.

Pomatomidae

Pomatomus saltatrix (Linnaeus)

The pelagic bluefish is rarely taken in shrimp trawls, and only one specimen, 277 mm. in standard length, was taken during this investigation. It was captured in seven fathoms of water off Punta Morros on February 14, 1951.

Rachycentridae

Rachycentron canadus (Linnaeus)

Small ling, under 2½ feet in length, were not uncommon in shrimp trawls, and they were recorded in 15 drags during February. Although small ling occur in the bay waters of Texas, I have never taken any ling except accidentally in trawls on the Texas coast (Hildebrand, 1954). One ling, 3 ft. long, was gilled in the binding of the foot rope during July. This specimen was taken in 13 to 14 fathoms during July. Ling will often swim around shrimp boats at anchor in the Gulf of Mexico and this was observed off Campeche during July.

Serranidae

Epinephelus morio (Cuvier and Valenciennes)

Three red grouper, one 116 mm. in standard length, in seven fathoms off Champoton and two 240 and 218 mm. in standard length, in 13 to 16 fathoms off Campeche, were caught.

Garrupa nigrita (Holbrook)

One warsaw, 55 mm. in standard length, was caught in 9 fathoms off Campeche on February 9, 1951. This fish was coal black except for white caudal and pectoral fins.

Serraniculus pumilio Ginsburg

A single fish, 24 mm. long, was taken in 13 fathoms west of Campeche on July 28, 1954. This recently described species has formerly been known only from the northern Gulf.

Diplectrum formosum (Linnaeus)

This sandfish was a very characteristic member of the fish fauna on the pink shrimp ground on Campeche Bank. It appeared in nearly every drag completed in 6 to 10 fathoms during February and at times it was the second species in abundance. This species has been reported several times from the northern Gulf, where it is apparently rare, although it appears to be more common in the northeastern Gulf (Reid, 1954).

Diplectrum bivittatum (Cuvier and Valenciennes)

In a previous paper (Hildebrand, 1954) I recorded the sandfish from the neighboring mud bottoms off Obregon as a separate species, *D. arcuarium.* The morphological differences between *bivittatum* and *arcuarium* are certainly not of specific magnitude as Ginsburg (1948) recognized. However, the difficulty resides in whether the three populations from Brazil, the West Indies, and the northern Gulf, respectively, should be treated as one species or two, and this cannot be clarified until specimens from critical areas are available. I did not collect a series of sandfishes from either Campeche or Obregon, so it is possible that the separation into two subspecies cannot be maintained.

D. formosum was the abundant form in a shallow water during February, and *D. bivittatum* was not found. However, during July *bivittatum* was the abundant species in 13 to 16 fathoms off Campeche.

Lutianidae

Lutianus griseus (Linnaeus)

Two mangrove snappers were taken in 8½ fathoms northwest of Campeche on February 6, 1951. Three additional snappers were taken in 13 fathoms west of Campeche on

July 28, 1951. This species is common throughout the western Gulf, and I have often seen this species while diving along the jetties at Port Aransas, where it apparently rarely reaches commercial size. The fartherest north fishery for this species in the western Gulf is at Punta Piedras, Tamaulipas in Laguna Madre, where a few thousand pounds are caught and exported to the United States each year.

Lutianus blackford Goode and Bean

Red snapper were recorded in 25 drags during February. The smallest snapper captured measured 75 mm. Ninety-five red snapper were taken in seven drags completed in 13 to 16 fathoms off Campeche during July. This is a much higher rate of capture than I found on the Texas coast (Hildebrand, 1954), but this is not unexpected because Campeche Bank has long been the most important snapper fishing ground in the Gulf of Mexico. In one drag 20 red snapper were caught and they ranged in length from 143 to 166 mm.

Lutianus synagris (Linnaeus)

Lane snappers were taken in 20 drags out of 53 attempted in 6 to 10 fathoms off Campeche and in several drags the species was listed as common. Thirty-three lane snappers were caught in 13 to 16 fathoms during July.

Ocyurus chrysurus (Bloch)

Longley (1941) lists the yellowtail as one of the most abundant species at Tortugas. However, it spends most of its life among the gorgonians and coral heads and would therefore rarely be taken in a trawl. The yellowtail appeared in the same drags as did the large loggerhead sponges. Five specimens were taken in 8½ fathoms northwest of Campeche during February, and two others were captured in 13 fathoms west of Campeche.

Rhomboplites auroruben Cuvier and Valenciennes

One bastard snapper was taken in 16 fathoms west of Campeche on July 27, 1951.

Haemulidae

Bathystoma aurolineaum rimator (Jordan and Swain)

The tomtate or redmouthed grunt was the most abundant fish on the pink shrimp grounds. It was recorded in every drag completed in 6 to 10 fathoms during February and often over ninety per cent of the fish caught belonged to this species. However, during July the tomtate was taken in every drag in 13 to 16 fathoms but it was not nearly as abundant as the mojarras and the bumper.

The tomtate is widely distributed in the Gulf of Mexico and Buller (1951) found this species as the most abundant fish in several drags in 19 fathoms off South Carolina. Hildebrand (1954) has used this species as an index species in describing the difference between the fish fauna of the northern and southern Gulf. It is never abundant in the northern Gulf and recent captures in the northwestern Gulf show that it is confined to the vicinity of snapper lumps. Young tomtates are presumably much more abundant in the clear water of the northeastern Gulf, and Jordan and Evermann (1898) list it as common around the wharfs and pilings.

Bathystoma striatum (Linnaeus)

A single specimen, 88 mm. in standard length, was taken in 13 to 16 fathoms off Campeche during July. I am indebted to Loren Woods for the identification of my specimens. Little is known of the distribution of this species, and Ginsburg (1948) examined only 4 specimens, three from Cuba and one from Haiti. Besides the firsh from Campeche, there are five additional fish that were captured on the Lobos Island fishing grounds in depths of 16 to 35 fathoms in the collection of the Institute of Marine Science.

Conodon nobilis (Linnaeus)

One barred grunt was captured in nine fathoms off Punta Morros on February 16, 1951. This species is predominantly a shallow water species, and it is taken in beach seines along the coast of Vera Cruz, Tamaulipas and Texas. Occasionally a few are imported into the United States, and I have examined several in fish houses in Brownsville that were caught off Third Pass on the Tamaulipas coast.

Orthopristis chrysopterus (Linnaeus)

The pigfish was captured in every drag completed in 6 to 10 fathoms during February. However, it was not nearly as abundant as the tomtate, except in three drags when it was listed as the most abundant fish. This species is common throughout the Gulf region, and the young are particularly characteristic in "grass" (chiefly *Thalassia*) beds along the Gulf coast (Reid, 1954, Hildebrand, 1954). Higman (1952) did not list this species in his report of live bait fishing in Florida Bay and Keys nor did Longley (1941) find it at Tortugas. This species was captured in five out of seven drags during July, but it was much less abundant than during February.

Haemulon plumieri (Lacépède)

Longley (1941) writes that this species is a nocturnal feeder and schools by day among the gorgonians and coral stacks off Tortugas. This species along with *Anisotremus virginicus* and *Pomacanthus arcuatus* was characteristic of loggerhead sponge bottom. This grunt was taken in two trawl hauls during February in 6 to 10 fathoms, and 110 fish were taken in 13 fathoms west of Campeche on July 28, 1951. This species occurs on the shallow water snapper lumps at least as far north as 24° 10′N. and it is not uncommon on Blanquilla reef off Cabo Rojo, Vera Cruz. However, it lives over bad trawling bottom and it is not a characteristic fish of the pink shrimp grounds.

Anisotremus virginicus (Linnaeus)

The porkfish, like the common grunt, is not an inhabitant of trawlable bottom. This species was recorded in two drags during February in 6 to 10 fathoms and 40 specimens were taken in 13 fathoms west of Campeche during July. These drags were characterized by the presence of loggerhead sponges. This species has not been reported from the Texas coast, and the farthest north that I have observed it is Blanquilla reef off Cabo Rojo, Vera Cruz.

Sparidae

Stenotomus caprinus Bean

This species was taken along with the Gulf blue crab, *Callinectes danae,* near the southwestern edge of Campeche Bank. It was listed as the third most abundant fish in this one drag in 10 fathoms. Such characteristic fishes of the pink shrimp grounds as the tomtate were rare in this drag. During July in 13 to 16 fathoms off Campeche this species was not uncommon and it was listed in six drags. All fish were small, and most were under two inches in length.

Calamus calamus (Cuvier and Valenciennes)

All my identifications are tentative, and they must remain so until the genus is revised. My specimens seem to fit the characteristics of several nominal species. In my collection there are four fishes identified as this species. Two were taken in 6 to 10 fathoms during February and the remaining two species were taken in 13 to 16 fathoms during July. Calamids were rare in 13 to 16 fathoms off Campeche.

Calamus penna (Cuvier and Valenciennes)

There are six specimens in the collection of the Institute of Marine Science that have been tentatively identified as this species. This species was relatively common during February when it was listed in 21 drags, and the largest number caught in a single drag was 120. This drag was completed in 8 to 9 fathoms off Punta Morros on February 15, 1951.

Lagodon rhomboides (Linnaeus)

Pinfish are abundant shorefishes around most of the Gulf coast, and the young are particularly abundant in grassy areas, although they do occur elsewhere. Pinfish were never abundant and forty per hour of trawling was the largest estimated catch. Pinfish were recorded in 25 drags during February and in two drags during July.

Archosargus probatocephalus (Walbaum)

Sheepshead are most abundant in the shallow bays along the north Gulf coast and they are caught in the greatest numbers in the bays from Corpus Christi, Texas to Tamiahua, Vera Cruz. In Texas sheepshead are usually marketed as drum *(Pogonias cromis)* and many are caught in the lower Laguna Madre during February, March and April.

Recently Ginsburg (1953) separated the sheepshead into two species. However, this separation was based on the number of transverse black bars. All adult sheepshead that I have examined from Port Aransas have the typical two stripes of *oviceps,* but there is one small specimen with three stripes. At Port Isabel, the number of sheepshead with three stripes is greater than at Port Aransas, and during one visit to a commercial fish house, I estimated that one in twenty had three stripes. Further south along the Mexican coast, my observations have been very sporadic, but both two and three stripers occur. The one specimen in the collection from Campeche has three stripes on one side and two stripes on the other. The number of stripes on the other sheepshead in the trawl were not observed. It seems best to synonymize *oviceps* with *probatocephalus*, although the varying frequency of color patterns in the various areas of the Gulf are noteworthy.

Only four sheepshead were taken in depths of six to ten fathoms. One of the crew members of the "San Jacinto" said they took many more during January, when they trawled through a "grassy" area.

Gerridae

Eucinostomus gula (Cuvier and Valenciennes)

Rapid field identification of the very similar species of mojarras is difficult. Twenty-one mojarras were brought back to the laboratory from Campeche Bank during February and they all proved to be *gula*. Mojarras were recorded in all drags completed on Campeche Bank and next to the tomtate they were the most abundant fish on the pink shrimp grounds. Nearly all the mojarras had ripe gonads and possibly they represented a spawning school. One fisherman told me that he observed a dense school of fish on his fathometer. He noted a great number of "silver perch" in his trynet so he ceased dragging the big net, but another boat dragging beside him continued fishing and he caught several tons of the little fish.

This species was also caught during July in 13 to 16 fathoms of water but it was not abundant.

Eucinostomus argenteus Baird and Girard

This species was recorded only in 13 to 16 fathoms off Campeche during July, but it is possible that this species was confused in the field with *gula* during February.

Diapterus rhombeus (Cuvier and Valenciennes)

This very distinctive mojarra is easily identified in the field. This species was only taken in 13 to 16 fathoms where it was very common, and in one drag in 16 fathoms it was the most common species. All specimens were small and the largest one measured was 100 mm. in standard length.

Mullidae

Mullus auratus Jordan and Gilbert

This species has apparently not been reported from the western Gulf. It is predominantly a West Indian species, and I recorded it in only three drags completed in 13 to 16 fathoms during July.

Sciaenidae

Corvula sanctae–luciae Jordan

Usually this species was taken singly, and I noted no evidence of schooling. I took this species is 15 drags completed in 6 to 10 fathoms on Campeche Bank during February, 1951. This West Indian species is unknown in the waters of continental United States.

Eques lanceolatus (Linnaeus)

This reef croaker is one of the most conspicuous fishes on the pink shrimp ground. I recorded it in 20 hauls on Campeche Bank during February and thirteen additional fish were caught in 13 to 16 fathoms during July.

Pareques acuminatus (Bloch and Schneider)

According to Longley (1941) this species rarely leaves the shadow of its overhanging reef shelter, and this undoubtedly explains the capture of isolated individuals in the trawl catches. Several were captured in 6 to 10 fathoms during February and one in 13 fathoms during July.

Micropogon undulatus (Linnaeus)

Two closely related species of croakers occur in the Gulf of Mexico. *M. undulatus* is the more northerly species and it occurs on the northwestern Gulf coast in tremendous abundance (Gunter, 1945), while *M. furnieri* is a West Indian species which enters the southern Gulf. Little is known about the relative importance of the two species along the east coast of Mexico. Hildebrand (1954) reported only *M. undulatus* from Obregon, where croakers were rare. However, there are reports that *M. furnieri* is the common croaker in the inshore waters from Tampico south. Since the two croakers were not always properly distinguished in the field, the data are grouped. Croakers were captured in 22 drags during February in 6 to 10 fathoms, but they made up an insignificant percentage of the catch. There is one preserved specimen of *M. undulatus* from 6 to 10 fathoms during February, and three specimens from 13 to 16 fathoms during July. Only 16 croakers were caught during July, and it is thought that they all were *M. undulatus.*

Micropogon furnieri (Desmarest)

A single specimen of the golden croaker is in the collection of the Institute of Marine Science that was collected in 6 to 10 fathoms during February. It is thought that the majority of the few croakers taken during February belonged to this species.

Menticirrhus americanus (Linnaeus)

Whiting were caught in over 95 per cent of the drags completed during February and it was the most abundant sciaenid on the pink shrimp grounds. Only twenty-six whiting were caught in 13 to 16 fathoms during July. Although this species was often the only commercial sized fish taken in the trawl, it never comprised more than 10 per cent of the catch.

Menticirrhus focaliger Ginsburg

Ten minkfish were caught in 6 to 10 fathoms during February. Hildebrand (1954) has previously discussed the distribution of this species in the Gulf.

Otolithidae

Cynoscion arenarius Ginsburg

Sand trout were rare in the trawl catches, and only this species was recorded in 6 to 10 fathoms during February. It was recorded in 30 drags during February and only two fish were taken in 13 to 16 fathoms during July.

Cynoscion nothus (Holbrook)

Four fish caught in 13 to 16 fathoms during July represent the entire catch of this fish on the pink shrimp grounds.

Ephippidae

Chaetodipterus faber (Broussonet)

Longley (1941) did not record this species from Tortugas, but the species ranges from Cape Cod to Brazil in suitable habitats. I recorded this species in fifteen hauls in 6 to 10 fathoms during February.

Chaetodontidae

Chaetodon ocellatus Bloch

Young angel fish less than 2½ inches long are not uncommon during the summer months at Port Aransas. It is confined to the jetties, and the predilection of this species for coral, rocks or other shelter explains its rarity in trawl catches. Three angel fish were caught during February in 6 to 10 fathoms and five specimens were caught in 13 fathoms west of Campeche on July 28, 1951. This species was associated with catches of coral and loggerhead sponges.

Pomacanthus arcuatus (Linnaeus)

The black angel fish is also a reef fish, and it was commonly captured with loggerhead sponges and coral. This species was recorded in five drags during February and in three during July. Most of the specimens were small and they still retained the banded pattern of the young.

Cataphracti

Scorpaenidae

Scorpaena brasiliensis Cuvier and Valenciennes

This was the only scorpaenid with an occipital pit collected on the shrimp grounds. Although it was recorded in thirty drags during February and in three drags in 13 to 16 fathoms during July, it was never abundant.

Scorpaena calcarata Goode and Bean

Although this is the most common scorpaenid in the inshore waters of the northwestern Gulf, as Gunter (1948) has shown, it is still more common on the shell sands of Campeche Bank. This species was recorded in 33 drags in 6 to 10 fathoms during February and it was much more abundant in 13 to 16 fathoms during July.

Triglidae

Prionotus ophryas Jordan and Swain

The family Triglidae has been recently revised by Ginsburg (1950) and independently by Teague (1951). There are some unresolved differences in species interpretation. Without commenting on the merits of the two revisions, Ginsburg's revision includes more data on Gulf triglids and his nomenclature has been followed. This triglid is widely distributed in the Gulf, but it is not known to occur in large concentrations (Hildebrand, 1954). This species was recorded in 13 drags during February in depths of 6 to 10 fathoms, and less than two dozen fish were taken in depths of 13 to 16 fathoms during July.

Prionotus scitulus Jordan and Gilbert

The slender searobin is one of the commonest and most characteristic fishes on the pink shrimp grounds off Campeche. This species was recorded in 49 drags out of 53 drags completed in 6 to 10 fathoms during February. It was not nearly so abundant in 13 to 16 fathoms during July.

Prionotus tribulus (Cuvier)

The collection contains a single female with enlarged ovaries. This specimen was taken in 10 fathoms during February. It was again recorded in 8 fathoms in a single drag. Primarily, this species is restricted to the bays and shallow water along shore (Gunter, 1945; Hildebrand, 1954), in the northern Gulf, and therefore it may be more common inshore of the area trawled.

Prionotus punctatus (Bloch)

This identification is only tentative, as my specimens seem to be intermediate between this species and *P. rubio.* Searobins were taken in 16 drags in 6 to 10 fathoms during February and in all seven drags during July in 13 to 16 fathoms.

Prionotus roseus Jordan and Evermann

Ginsburg (1950) lists this species from 22 to 38 fathoms and he examined a number of specimens from the Florida Peninsula, Cabo Catoche, Yucatan and the northern Gulf coast. Thirteen specimens were recorded in 13 to 16 fathoms off Campeche.

Bellator militaris (Goode and Bean)

Ginsburg (1950) found that this species lived offshore and he examined specimens that were caught in depths of 22 to 60 fathoms. Six soldier searobins were taken in depths of 13 to 16 fathoms during July.

Dactylopteridae

Dactylopterus volitans (Linnaeus)

The flying gurnard was taken in 11 drags in 6 to 10 fathoms during February and a single specimen was taken in 13 to 16 fathoms during July.

Pharynognathi

Labridae

Lachnolaimus maximus (Walbaum)

Hogfish were recorded only twice during February in depths of 6 to 10 fathoms. This species ranges at least as far north as North Carolina on the Atlantic coast, but the northward extent of its range in the western Gulf is not known.

Scaridae

Cryptotomus ustus (Cuvier and Valenciennes)

Although there is undoubtedly a varied fauna of parrotfishes among the coral reefs, and Gunter (1952) has recorded two species from here, only this species was recognized in the trawl catches. This fish was recorded in 19 drags in depths of 6 to 10 fathoms during February. However, during July it was much more abundant and as many as 100 fish were captured in a single drag in depths of 13 to 16 fathoms.

Discocephali

Echeneidae

Echeneis naucrates Linnaeus

Small remoras, 20 to 400 mm. long, were taken repeatedly on the shrimp grounds during February, although the larger fish to which they may have been attached were never caught. I recorded this species in 29 drags completed in 6 to 10 fathoms during February. Only three fish were caught in 13 to 16 fathoms during July.

Jugulares

Opisthognathidae

Opisthognathus macrognathum Poey

Four jawfish were captured in 10 fathoms on Campeche Bank during February, 1951.

Brotulidae

Brotula barbata (Bloch and Schneider)

This species was common on the mud bottom off Obregon, Mexico (Hildebrand, 1954), but it was rare on Campeche Bank. Three fish were caught in depths of 13 to 16 fathoms during July.

Ophidiidae

Lepophidium brevibarbe (Cuvier)

This species was very abundant on the neighboring brown shrimp grounds off Obregon, Mexico, but only 12 fish were captured in depths of 13 to 16 fathoms during July on Campeche Bank.

Ophidion holbrooki (Putman)

This cusk eel was not common and it was recorded from two drags during February in depths of 6 to 10 fathoms and from one drag during July in depths of 13 to 16 fathoms. One specimen caught in eight fathoms had been eating small gastropods.

Batrachoididae

Opsanus sp.

One oysterdog was taken in nine fathoms off Punta Morros on February 16, 1951.

Nautopaedium porosissimum (Cuvier and Valenciennes)

Midshipmen were very abundant on the neighboring mud bottoms off Obregon (Hildebrand, 1954). It was taken in all drags completed in 13 to 16 fathoms during July off Campeche, but it was not abundant. Midshipmen were recorded from only 10 drags in 6 to 10 fathoms during February.

Plectognathi

Balistidae

Balistes capriscus (Gmelin)

While never abundant in any single drag, triggerfish appear in the trawl catches in the western Gulf with great regularity. This species was much more common during July in 13 to 16 fathoms than during February when I recorded it in only 10 drags out of 53 completed.

Monacanthidae

Monacanthus hispidus (Linnaeus)

Foolfish were very common on the pink shrimp grounds. I took this species in 43 drags in depths of 6 to 10 fathoms during February and in all seven drags in depths of 13 to 16 fathoms during July.

Monacanthus ciliatus (Mitchill)

Reid (1954) found that this species was more abundant during the winter months at Cedar Key and the reverse was true for *M. hispidus.* No concentrations of this species were found on the pink shrimp grounds and it was recorded in three drags during February and from one drag in 15 to 16 fathoms during July.

Alutera guentheriana Poey

This large gray filefish with high fin counts (D. 46, A. 49) was the rarest filefish in the trawl catches. It was recorded in five drags and only one specimen was taken per drag.

Alutera schoepfi (Walbaum)

This filefish varied from nearly black to a light gray in color and next to *M. hispidus* it was the commonest filefish on the pink shrimp grounds. Common filefish were taken in 23 drags during February and in three drags during July.

Alutera ventralis Longley

This species was taken in 8 to 10 fathoms during February and in 13 to 16 fathoms during July, but it was never common.

Ostracidae

Lactophrys tricornis (Linnaeus)

Cowfish are abundant at Campeche, and they were recorded in every drag completed on Campeche Bank in depths of 6 to 16 fathoms. During February this species often ranked among the top three species in abundance. It is a very hardy fish and survives better than any other fish on the deck of the shrimp trawlers. They are a source of some amusement to the fishermen, as they will wriggle their tails very rapidly when put back into the water and take off as if jet propelled.

Tetradontidae

Lagocephalus laevigatus (Linnaeus)

Rabbitfish were taken in three drags during February and in one drag during July.

Sphoeroides nephelus Goode and Bean

The common puffer in the northern Gulf has been reported under the name of *S. marmoratus, S. maculatus* and *S. nephelus* in recent years. Some of my specimens seem to be identical with the puffer from the Texas coast. In the northwestern Gulf this species is a small fish and the largest that I have measured was 120 mm. long. Gunter (1945) gives a maximum size of 131 mm. for the Texas coast puffer. One of my specimens from Campeche with nearly ripe ovaries was only 91 mm. long.

This small puffer was recorded in 10 drags during February and in 6 drags during July in 13 to 16 fathoms.

In addition there is a larger puffer (the largest measured 190 mm.) which resembles *S. nephelus* in spination and meristic characters, and differs from it in reaching a large size and in coloration. This larger puffer was not common, and only three were recorded.

Sphoeroides dorsalis Longley

Several specimens were caught in 13-16 fathoms during July.

Sphoeroides testudineus (Linnaeus)

This large puffer was not uncommon in the trawl catches during February, when it was recorded in 27 drags. It was not taken in 13 to 16 fathoms during July. It was most abundant on the shell sand bottom off Punta Morros in depths of six to nine fathoms.

Sphoeroides spengleri (Bloch)

Longley (1941) reported this very distinctively marked puffer as common on the grass flats off Tortugas. Reid (1954) reported this species from Cedar Key and I found it off Port Isabel (Hildebrand, 1954). I took five puffers in 13 fathoms off Campeche on July 28, 1951.

Diodontidae

Chilomycterus schoefi (Walbaum)

Spiny boxfishes were taken in only eight hauls during February, and at no time were more than 8 fish taken per drag. Five specimens were trawled in 13 to 16 fathoms during July.

Pediculati

Ogcocephalidae

Ogcocephalus cubifrons (Richardson)

One species of batfishes with 12 to 13 pectoral rays and a short snout was caught. This species was trawled in twenty drags during February and twenty-one fish were captured in 13 to 16 fathoms during July.

Halieutichthys aculeatus (Mitchill)

The range of this species is predominantly at greater depths than those fished on Campeche Bank (Hildebrand, 1954). A single example was taken in 16 fathoms off Campeche on July 27, 1951.

Antennaridae

Antennarius scaber (Cuvier)

The common frogfish was recorded in only 10 drags in six to ten fathoms during February and four additional specimens were captured in 13 to 16 fathoms during July.

Antennarius nuttingi Garman

A single black frogfish was caught in 10 fathoms off Campeche on February 7, 1951.

GENERAL DISCUSSION OF THE FAUNA

If the small species of mollusks are excluded, a very few species of gastropods and pelecypods make up the bulk of the trawl catches. Although the species may be few in number and represent only a small percentage of the total number of species on the grounds, the otter trawl may be filled with mollusk shells or break under their weight. Such a condition is not encountered on the mud or sand bottoms where the brown and white shrimp thrive. Shell piles or ridges may exist in the region of the brown and white shrimp fisheries such as the shell ridge at Chiltepec (western edge of the Obregon grounds), the shell "piles" off Port Isabel, Freeport and Sabine and the shell "ridge" off Big Constance Bayou, Louisiana, but these are very restricted in area and do not produce large quantities of shrimp. Unfortunately, little is known about these concentrations of shell and, therefore, they cannot be compared with the Campeche area. The concentrations of shell or conchs were overcome by modifications in gear. First the leads were removed and a "jumper" chain was tied about 12 inches in front of the foot rope, and secondly the chafing gear was made more substantial than that used on the mud bottom of the brown shrimp grounds.

Twenty-eight species of gastropods are discussed in this report. A few species such as *Fusinus couei, Conus spurius atlanticus, Scaphella junonia,* and *Cassis madagascariensis* were very conspicuous because of shape, size or coloration, but none of these species were abundant. However, twenty large *Cassis madagascariensis* conchs in a single drag, and that many were caught several times, would greatly increase the bulk of the catch. This large conch seems to be locally concentrated in abundance and not widely and sparingly distributed over the shrimping grounds. *Scaphella junonia* is not an abundant snail, but even if only five specimens were taken each night per boat and sometimes there are 300 or more boats fishing, it becomes very clear how the curio shops are kept supplied with this species.

Several small gastropods, particularly *Crepidula plana, Crepidula aculeata* and *Crucibulum,* were abundant because they attach themselves to larger shells.

Strombus alatus, Pleuroploca gigantea, Busycon coarctatum, Xancus angulatus, Fasciolaria tulipa and *Ficus communis* were the dominant species on the pink shrimp grounds in depths of 6 to 16 fathoms. Although numerically *Strombus alatus* was the most abundant species, this may be in part due to the thickness and durability of the shell. Hermit crabs, particularly *Petrochirus bahamensis,* lived in the empty shells, and often ninety per cent of the shells contained hermit crabs. *Busycon coarctatum* was widely distributed and very abundant on the grounds. *Xancus angulatus* seemed to be more abundant in deeper water; the greatest number recorded in a single drag was 500 in 13 fathoms of water off Campeche, Mexico during July. All the species listed as dominant on the pink shrimp ground are unknown on the brown shrimp grounds, except *Fasciolaria tulipa* and *Pleuroploca gigantea* which are very rare, and *Strombus alatus,* which may be locally abundant (see Hildebrand, 1954). Common species on the white shrimp grounds, such as *Busycon spiratum* and *Busycon contrarium,* are rare on the pink shrimp grounds.

Pelecypods are rather rare in the trawl catches on the pink shrimp ground because of the modifications in the trawls. Attached species such as *Ostrea equestris* and *Chama* sp. were sometimes abundant. *Mercenaria campechiensis, Dosinia elegans, Arca zebra* and *Arca lienosa,* while not abundant, were repeatedly captured. The amount of dead and broken shell of *Mercenaria campechiensis* indicates that there may be beds of this species offshore.

Octopus vulgaris was much more abundant than off the Texas coast. It used old shells of *Pleuroploca gigantea* for refuge.

Two species of stomatopods were common on Campeche Bank but *Squilla empusa* was much more abundant. This species seems to prefer water of near oceanic salinity (Gunter, 1950) and it ranges widely on the continental shelf in the western Gulf of Mexico. It was found abundant on the brown shrimp grounds (Hildebrand, 1954) and according to Perez-Farfante (1954) this species is abundant on the pink shrimp grounds off Batabano, Cuba. The other squillid, *Lysiosquilla scabricauda,* is a large and distinctive species and, although it occurs in the northwestern Gulf, it is more abundant on Campeche Bank.

The pink shrimp, *Penaeus duorarum,* was the dominant crustacean on the grounds and the most abundant single species in the trawl catches. *Sicyonia brevirostris* was common, but the other three species, *Sicyonia dorsalis, Trachypeneus constrictus* and *Solenocera atlantidis,* were rare. The adults of the pink shrimp show a decided preference for calcareous sediments, and only a few individuals are taken on mud bottom, although there is some evidence that they do occur on hard sand bottom, particularly in non-turbid waters (Hildebrand, 1954).

As on the white and brown shrimp grounds and apparently nearly everywhere on the continental shelf of the Gulf of Mexico, the family Portunidae predominated in the catches of crabs. However, the Gulf blue crab, *Callinectes danae,* so abundant on the brown shrimp grounds, occurred only sparingly on the southern edge of the banks, and

Portunus spinimanus and *Portunus gibbesi* predominated. According to Siebenaler (1953) a portunid also predominates on the Tortugas shrimp grounds, although the only species he lists is *Cronius ruber.*

The echinoderms were more varied but scarcely more numerous than on the white or brown shrimp grounds in the northern Gulf of Mexico. The most conspicuous member of the phylum was *Oreaster reticulatus* and this large starfish does not occur on the Texas coast. Another conspicuous member of the fauna was a stinking sea-cucumber, *Asticopus multifidus.* Both *Arbacia* and *Lytechinus* occur along the Texas coast, but

TABLE 2

Species of Fishes Caught in 6–10 Fathoms on Campeche Bank During February

Sphyrna tiburo
Rhinobatus lentiginosus
Narcine brasiliensis
Raja texana
Dasyatis americana
Gymnura micrura
Urolophus jamaicensis
Albula vulpes
Sardinella anchovia
Harengula pensacolae
Opisthonema oglinum
Brevoortia gunteri
Anchoa hepsetus
Gymnothorax vicinus
Synodus foetens
Trachinocephalus myops
Ancylopsetta quadrocellata
Syacium gunteri
Syacium papillosum
Cyclopsetta chittendeni
Cyclopsetta fimbriata
Citharichthys macrops
Etropus crossotus
Bothus ocellatus
Gymnachirus texae
Gymnachirus williamsoni
Achirus lineatus
Symphurus plagiusa
Symphurus urospilus
Syngnathus louisianae
Hippocampus hudsonius
Sphyraena guachancho
Polydactylus octonemus
Decapterus punctatus
Caranx crysos
Caranx hippos
Caranx latus
Caranx ruber
Trachinotus carolinus
Chloroscombrus chrysurus
Vomer setapinnis
Seriola dumerili
Pomatomus saltatrix
Scomberomorus maculatus
Rachycentron canadus
Epinephelus morio
Garrupa nigrita
Diplectrum formosum
Lutianus griseus
Lutianus blackfordi
Lutianus synagris
Ocyurus chrysurus
Conodon nobilis
Bathystoma a. rimator
Orthopristis chrysopterus
Haemulon plumieri
Anisostremus virginicus
Stenotomus caprinus
Calamus calamus
Calamus penna
Lagodon rhomboides
Archosargus probatocephalus
Eucinostomus gula
Corvula sanctae-luciae
Eques lanceolatus
Pareques acuminatus
Micropogon undulatus
Micropogon furnieri
Menticirrhus americanus
Menticirrhus focaliger
Cynoscion arenarius
Chaetodipterus faber
Chaetodon ocellatus
Pomacanthus arcuatus
Scorpaena brasiliensis
Scorpaena calcarata
Prionotus ophryas
Prionotus scitulus
Prionotus tribulus
Prionotus punctatus
Dactylopterus volitans
Lachnolaimus maximus
Cryptotomus ustus
Echeneis naucrates
Opisthognathus macrognathum
Ophidion holbrooki
Opsanus sp.
Nautopaedium porosissimum
Balistes capriscus
Monacanthus hispidus
Monacanthus ciliatus
Alutera schoepfi
Alutera ventralis
Alutera guentheriana
Lactophrys tricornis
Lagocephalus laevigatus
Sphoeroides nephelus
Sphoeroides testudineus
Chilomycterus schoepfi
Antennarius scaber
Antennarius nuttingi
Ogcocephalus cubifrons

very little is known concerning the distribution of sea urchins along the shores of the western Gulf.

Ascidians were varied and numerous but in no drag did they dominate the catch.

During 106 hours of trawling on Campeche Bank, 125 species of fishes belonging to 47 families were captured. Seasonally the trawling was distributed as follows: 88 hours during February in depths of 6 to 10 fathoms and 18 hours during July in depths of 13 to 16 fathoms. Almost all drags were completed in the area lying off the coast between the towns of Campeche and Champoton, Mexico. Several drags were completed a few miles north and south of the above towns respectively.

TABLE 3

Species of Fishes Caught in 13–16 Fathoms on Campeche Bank During July

Carcharhinus acronotus
Carcharhinus obscurus
Sphyrna tudes
Rhinobatus lentiginosus
Raja texana
Gymnura micrura
Sardinella anchovia
Synodus foetens
Synodus intermedius
Trachinocephalus myops
Ancylopsetta quadrocellata
Syacium gunteri
Syacium papillosum
Cyclopsetta chittendeni
Citharichthys macrops
Etropus crossotus
Bothus ocellatus
Gymnachirus williamsoni
Symphurus plagiusa
Symphurus civitatum
Symphurus diomedianus
Symphurus urospilus
Polydactylus octonemus
Sarda sarda
Poronotus triacanthus
Decapterus punctatus
Selar crumenophthalmus
Chloroscombrus chrysurus
Vomer setapinnis
Rachycentron canadus
Epinephelus morio
Serraniculus pumilio
Diplectrum formosum
Diplectrum bivittatum
Lutianus griseus
Lutianus blackfordi
Lutianus synagris
Ocyurus chrysurus
Rhomboplites aurorubens
Bathystoma a. rimator
Bathystoma striatum
Haemulon plumieri
Orthopristis chrysopterus
Anisotremus virginicus
Stenotomus caprinus
Calamus calamus
Lagodon rhomboides
Eucinostomus gula
Eucinostomus argenteus
Diapterus rhombeus
Mullus auratus
Eques lanceolatus
Pareques acuminatus
Micropogon undulatus
Menticirrhus americanus
Cynoscion arenarius
Cynoscion nothus
Chaetodon ocellatus
Pomacanthus arcuatus
Scorpaena brasiliensis
Scorpaena calcarata
Prionotus ophryas
Prionotus scitulus
Prionotus punctatus
Prionotus roseus
Bellator militaris
Dactylopterus volitans
Cryptotomus ustus
Echeneis naucrates
Brotula barbata
Lepophidium brevibarbe
Ophidion holbrooki
Nautopaedium porosissimum
Balistes capriscus
Monacanthus hispidus
Monacanthus ciliatus
Alutera schoepfi
Alutera ventralis
Lactophrys tricornis
Lagocephalus laevigatus
Sphoeroides dorsalis
Sphoeroides nephelus
Sphoeroides spengleri
Chilomycterus schoepfi
Antennarius scaber
Ogcocephalus cubifrons
Halieutichthys aculeatus

Numerical data were gathered for 8 hours and 30 minutes of trawling time during February and 5 hours and 5 minutes of trawling time during July. These data are listed in Table 4 and Table 5. These tables are self-explanatory and only a few comments will be made. First, only 56 species were recorded out of 102 captured during February in these drags. The species not encountered were rare and they only sporadically appeared in the other drags. However, the fishing log contains information for each drag on the first three or four species in abundance and from this data it is clear that *Bathystoma*

TABLE 4

Relative Abundance of Fishes in 6–10 Fathoms on Campeche Bank During February*

Bathystoma a. rimator	4,700	Citharichthys macrops	11
Chloroscombrus chrysurus	4,250	Hippocampus hudsonius	10
Eucinostomus gula	2,050	Anchoa hepsetus	10
Diplectrum formosum	1,360	Prionotus ophryas	10
Prionotus scitulus	1,070	Chaetodipterus faber	10
Etropus crossotus	800	Symphurus spp.	10
Orthopristis chrysopterus	500	Echeneis naucrates	6
Syacium spp.	220	Brevoortia gunteri	6
Lactophrys tricornis	215	Menticirrhus focaliger	4
Bothus ocellatus	200	Micropogon sp.	3
Menticirrhus americanus	150	Raja texana	2
Scorpaena calcarata	115	Rhinobatus lentiginosus	2
Lagodon rhomboides	60	Ancylopsetta quadrocellata	2
Achirus lineatus	55	Corvula sanctae-luciae	2
Synodus foetens	55	Sphyraena guachancho	2
Scorpaena brasiliensis	54	Harengula pensacolae	1
Opisthonema oglinum	50	Sardinella anchovia	1
Sphoeroides testudineus	32	Cyclopsetta chittendeni	1
Lutianus blackfordi	32	Caranx ruber	1
Cynoscion arenarius	30	Pomacanthus arcuatus	1
Monacanthus hispidus	30	Prionotus tribulus	1
Polydactylus octonemus	22	Prionotus punctatus	1
Eques lanceolatus	22	Dactylopterus volitans	1
Calamus calamus	20	Balistes capriscus	1
Rachycentron canadus	21	Opisthognathus macrognathum	1
Lutianus synagris	18	Alutera guentheriana	1
Alutera schoepfi	17	Ogcocephalus cubifrons	1
Sphoeroides nephelus	13	Antennarius scaber	1

* Data from 8 hours and 30 minutes of trawling.

TABLE 5

Relative Abundance of Fishes in 13–16 Fathoms on Campeche Bank During July*

Stenotomus caprinus**	2,750	Prionotus punctatus	20
Chloroscombrus chrysurus	800	Lutianus blackfordi	16
Eucinostomus gula	500	Monacanthus hispidus	15
Syacium gunteri	420	Lepophidium brevibarbe	11
Bathystoma a. rimator	270	Mullus auratus	10
Diplectrum bivittatum	250	Trachinocephalus myops	10
Diapterus rhombeus	160	Scorpaena brasiliensis	10
Etropus crossotus	150	Rhinobatus lentiginosus	7
Bothus ocellatus	150	Ancylopsetta quadrocellata	6
Cryptotomus ustus	150	Ogcocephalus cubifrons	6
Syacium papillosum	100	Lutianus synagris	6
Citharichthys macrops	100	Chilomycterus schoepfi	3
Scorpaena calcarata	50	Eques lanceolatus	3
Nautopaedium porosissimum	40	Prionotus roseus	3
Lactophrys tricornis	35	Brotula barbata	3
Polydactylus octonemus	35	Micropogon undulatus	1
Symphurus spp.†	25	Rachycentron canadus	1
Synodus foetens	24	Gymnachirus williamsoni	1
Sphoeroides nephelus	23	Prionotus ophryas	1
Balistes capriscus	20	Prionotus arcuatus	1
Cyclopsetta chittendeni	20	Menticirrhus americanus	1

* Data from 5 hours and 5 minutes of trawling.
** All juveniles (less than 3 inches in total length).

TABLE 6

The Number of Species of Fishes Caught in Trawls on the Pink and Brown Shrimp Grounds During July and August, 1951

Date	Location	Depth in Fathoms	No. Hours Trawled	No. Species
7/29/51–8/6/51	Obregon	13–20	80 hours	85
7/5–11/51	Off Padre Island, Texas	12–18	65 hours 15 min.	69
7/27–29/51	Off Campeche	13–16	18 hours	87

TABLE 7

The Ten Most Abundant Species of Fishes on the Obregon, Campeche and South Texas Grounds During July and August, 1951

South Texas*	Obregon*	Campeche
Poronotus triacanthus	Paracentropristes pomospilus	Stenotomus caprinus
Syacium gunteri	Nautopaedium porosissimum	Chloroscombrus chrysurus
Micropogon undulatus	Synodus spp.†	Eucinostomus gula
Cyclopsetta chittendeni	Syacium gunteri	Syacium gunteri
Cynoscion nothus	Lepophidium brevibarbe	Bathystoma a. rimator
Synodus foetens	Prionotus rubio	Diplectrum bivittatum
Citharichthys spilopterus	Diplectrum arcuarium	Diapterus rhombeus
Menticirrhus americanus	Trichiurus lepturus	Etropus crossotus
Prionotus rubio	Cyclopsetta chittendeni	Bothus ocellatus
Cynoscion arenarius	Cynoscion arenarius	Cryptotomus ustus

* Data from Hildebrand (1954).
† Predominantly *Synodus foetens*.

a. rimator was much more abundant on the grounds than is suggested by the tables. In nearly every drag it was the most abundant fish, and often it comprised nearly 90 per cent of the fishes by number. Forty-two out of the 86 species caught during July are listed in the numerical data for that month. None of the omitted species were abundant in any of the drags not counted. Here it is necessary to comment that all the porgies, *Stenotomus caprinus*, were juveniles and they made up only a small part of the catch by weight. From the abundance rankings in the uncounted drags, it appears that *Diapterus rhombeus* should be ranked higher, perhaps second or third.

Nearly all the fishes were small, and often not more than 6 fish would measure 8 inches or more in length. However, it is shown by my data that the mojarras, *Eucinostomus gula* and *Diapterus rhombeus*, occur in large schools and the tomtate, *Bathystoma a. rimator* is extremely abundant.

The only closely comparable data from other shrimping grounds in the Gulf of Mexico are the records of trawl hauls off Obregon and south Texas during July and August, 1951 (Hildebrand, 1954). Although the time spent trawling and the bathymetric range were both greater on the south Texas and Obregon grounds, the number of species of fishes were greater in the trawl catches on Campeche Bank.

Only *Syacium gunteri* is common to all three lists and its abundance on the pink shrimp ground is not as great as on the mud bottom of the brown shrimp ground. Although the number one species on the Campeche list is one of the most abundant species in the northern Gulf, only small juveniles (under 3 inches in total length) were caught on the banks. Especially noteworthy is the disappearance of the croakers (Sciaenidae) and the weakfishes (Otolithidae) from the abundant species and the greatly increased abundance of the Gerridae, Haemulidae and Carangidae.

SOME GENERAL CONSIDERATIONS

Certain Zoogeographical Data

No attempt was made to correlate the various species of fishes and invertebrates with physical conditions. Undoubtedly the type of substratum is very important and Springer and Bullis (1954) emphasize this by dividing the Gulf of Mexico into an Eastern and Western area on the basis of calcareous (biogenous) and clastic (terrigenous) sediments on the continental shelf. The boundaries of these two areas are placed at Pensacola, Florida and near Sanbancuy in the Gulf of Campeche. This line divides the shrimp fisheries fairly well. The pink shrimp predominates on calcareous bottom and the brown and white shrimp predominate on mud bottom. However, there are outliers in both areas such as the Apalachicola Bay white shrimp fishery and the coral reefs along the coast of Mexico from Vera Cruz to Cabo Rojo. Furthermore, the pink shrimp is widely distributed outside of Springer's Eastern Gulf and there is some evidence that they are abundant in some years along the northeastern coast of Mexico. Consequently, whether this division is any better than a north-south division for comparing the fauna is doubtful, but it cannot be decided on the basis of existing published information. I have shown (Hildebrand, 1954) that most of the species listed by previous authors as occurring only in the eastern or western Gulf occur in both areas.

Certainly the fauna changes from north to south and although many of these changes are gradual, the main break probably occurs in the vicinity of Tampico in the western Gulf. This is shown by the position of the shallow water coral reefs, and the change in the commercial fishery from one relying predominantly on the croakers (Sciaenidae) and weakfishes *(Cynoscion)* to one producing many robalos (Centropomidae) and mojarras (Gerridae). Off the shallow shelf in the northern Gulf there are the snapper lumps and as Lowman (1949) has shown, the foraminifera on these topographic irregularities may show affinities with other regions. For example, on one lump off the mouth of Southwest Pass of the Mississippi River, he found that it was dominated by *Amphistegina,* an abundant genus in the clear water off the coast of western Florida. This emphasizes that the species list may be very similar in many parts of the Gulf, but the quantitative aspects of the fauna may vary greatly.

Bottom Communities

Except for the oyster community all the four communities described by Hedgpeth (1954) occur in adjacent areas on Campeche Bank. The coral community, of course, cannot be sampled by a trawl and it is not characterized. The sponge community is dominated by the large loggerhead sponge, *Spheciospongia vesparia,* and this community was also avoided by the shrimp fishermen. However, several times we inadvertently trawled this community and each time the net was damaged. The characteristic fishes on the sponge bottom were the common grunt, *Haemulon plumieri,* yellowtail, *Ocyurus chrysurus,* the porkfish, *Anisoteremus virginicus,* and the black angelfish, *Pomacanthus arcuatus.* Pink shrimp were common but whether they are ever as abundant as on clear bottom could not be determined. All the fishes listed from the sponge community are common on coral reefs, and this supports Hedgpeth's opinion that the sponge community may be only a sub-community of the coral reefs. The shrimp community is variable because in some areas there are expanses of clear bottom and in others there are accumulations of mollusks. However, it can be briefly characterized as a *Penaeus duorarum-Bathystoma aurolineatum rimator* community, although this may be modified somewhat when the area is investigated at all seasons.

Productivity of Commercial Trawl Fisheries

Burkenroad (1951) has reviewed the records of productivity of commercial fishes by trawl fisheries in various parts of the world. However, the literature is very scanty, and none of it seems to be directly comparable with my data.

In computing the number of acres swept by the shrimp trawl, the same arbitrary method was used as in the computation on the brown and white shrimp grounds (Hildebrand, 1954). That is, the speed of the trawler was estimated at 2½ knots and the effective sweeping width of the trawl was estimated at 80 per cent of the foot rope (lead line) length. Shrimp are not like most other commercial species; they are primarily an annual or perhaps biennial crop. The catch per hour of trawling or acre of bottom swept varies greatly from one season to another and it is, of course, related to fishing effort. The catch varied from 1.2 pounds per acre in April to 7.3 pounds in July and August on the brown shrimp grounds in the Gulf of Mexico (Hildebrand, 1954), while on the pink shrimp grounds the rate was 7.8 pounds per acre during February and 5.4 pounds per acre during July. Since that time the catch per unit of effort is known to have declined greatly but published data for comparison are not available.

Undoubtedly, the catch of finfishes could have been greatly increased by fishing specifically for them. However, the poundage of finfishes caught exceeded the catch of shrimp. Nearly all the fishes were small and the number of panfishes were chiefly limited to a few species such as the whitings (Menticirrhus), sheepshead (*Archosargus)*, porgy *(Calamus)* and croakers *(Micropogon)* which were caught in very small amounts. It would seem that a finfish fishery on the banks is not possible, outside of the very important snappers and groupers, if filets sized fishes are required. However, if the size does not matter, as for example in products like East Indian trassi, there is a large resource of protein food available. It is shown by my data that the mojarras, *Eucinostomus gula* and *Diapterus rhombeus,* occur in large schools and the tomtate, *Bathystoma a. rimator*, is extremely abundant, and these fishes could be readily exploited by a trawl fishery.

Interspecific Competition

Only in the Gulf of Campeche do the three important species of commercial shrimp support fisheries in contiguous areas. Although the ranges of the three species overlap, and presumably all three species may be at times taken in a single drag, their preferred environmental niches seem distinct enough to keep competition at a minimum. However, changes in physical environment such as variations in salinity may favor one species more than another.

The young of the pink shrimp, *Penaeus duorarum,* prefers water of rather high salinity and plenty of vegetation for cover. The young of the white shrimp, *Penaeus setiferus,* seems to thrive best on mud bottom in waters of low salinity, and as the shrimp grows, it moves into deeper and more saline waters (Gunter, 1950). The young of the brown shrimp. *Penaeus aztecus,* also thrives on mud bottom, but it seems to thrive better in water of high salinity than does the white shrimp. However, both species have a wide range of salinity tolerance. It would, therefore, appear that competition would be greatest among the young of the white and brown shrimp, and this may explain the different peaks in abundance of the young found by Gunter (1950) in Texas bays. Presumably, high rainfall and low salinity is more favorable to the white shrimp than to the other two species, but this cannot be proven by the shrimp landings because no fishery for brown shrimp existed on the Gulf coast during the low salinity years.

The adults of the pink shrimp prefer calcareous sediments while the other two species occur in greatest abundance on mud bottom. However, the bathymetric distribution of the adults of the whites and browns is different. The browns occur most abundantly in water deeper than 12 fathoms while the white shrimp are common in the shallower water. There may be some competition for food where the ranges of the two overlap, but nothing is known of the food habit of either species. However, the difference in the habits of the two as shown by the trawl fishery would tend to reduce competition. The white shrimp is caught primarily during the day and the brown shrimp at night. Although the bathymetric range of the white and pink shrimp is the same, it is apparent that preferred substrate and the associated food supply of the two species are different. Furthermore, the pink shrimp is caught chiefly at night, while the white is caught during the daytime.

SUMMARY

1. During February, 1951 and again during July, 1951 the fauna of the shrimp beds of Campeche Bank were sampled by the trawls of the shrimping fleet. Sixty trawl hauls were made, covering a period of 104 hours of continuous trawling.

2. Specimens were counted and identified in the field and some were brought ashore for further study.

3. The shrimping grounds on Campeche Bank were delineated and described. The faunal complex or bottom community was described and given a community designation in terms of the most abundant animals caught. The relative abundance of all species of fishes and the large invertebrates is discussed and compared with the shrimping grounds in other parts of the Gulf. In brief, the bottom community of the Campeche shrimp grounds may be called a *Penaeus duorarum-Bathystoma aurolineatum rimator* community.

4. Each species is discussed individually and various natural history notes including bathymetric distribution are given.

5. Data were gathered on the quantitative distribution of pink shrimp by pounds per acre of bottom trawled. During February, the catch averaged 7.5 pounds per acre and during July the catch was 5.4 pounds per acre.

6. There is a pronounced difference in the fauna of the pink shrimp grounds and the neighboring brown shrimp grounds. The mojarras (Gerridae) and the grunts (Haemulidae) are much more abundant on the Campeche grounds than off Obregon or in the northern Gulf.

7. The commercial shrimp fisheries in the Gulf of Campeche are discussed with special emphasis on the habitat differences that may lessen interspecific competition between the three important commercial species.

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LITERATURE CITED

Abbott, R. Tucker. 1954. American seashells. New York: D. Van Nostrand Co., XIV, 541 pp.

Anderson, W. W., M. J. Lindner and J. E. King. 1949. The shrimp fishery of the southern United States. Comm. Fish Rev. 11(2): 1–17.

Bigelow, H. B. and W. C. Schroeder. 1954. Fishes of the Western North Atlantic. Part 2. Sawfishes, guitarfishes, skates and rays. Mem. Sears Found. Mar. Res. 2: XV, 588 pp.

Broad, Carter. 1950. The shrimp fishery of the Florida Keys. Univ. North Carolina Inst. Fish. Res. (Mimeo.): 1–13.

Buller, R. J. 1951. A fishery survey of southern coastal waters. U. S. Fish and Wildlife Service Special Scientific Report—Fisheries No. 58: 1–21.

Burkenroad, M. D. 1939. Further observations on Penaeidae of the northern Gulf of Mexico. Bull. Bingham Oc. Coll. 6(6): 1–62.

Burkenroad, M. D. 1949. Occurrence and life histories of commercial shrimp. Science 110: 688–689.

Burkenroad, M. D. 1951. Some principles of marine fisheries biology. Publ. Inst. Mar. Sci. 2(1): 177–212.

Campbell, T. N. 1952. The Kent-Crane site: a shell midden on the Texas coast. Bull. Texas Archeol. Paleo. Soc. 23: 39–77.

Clench, W. J. 1942. The genus *Ficus* in the Western Atlantic. Johnsonia (1(2): 1–2.

De Sylva, D. 1954. The live bait shrimp fishery of the northeast coast of Florida. Fla. Board of Conservation Technical Series No. 11: 1–35.

Ginsburg, Isaac. 1948. Some Atlantic populations related to *Oiplectrum radiale* (Serranidae) with description of a new subspecies from the Gulf coast of the United States. Copeia (4): 266–270.

Ginsburg, Isaac. 1948. The species of *Bathystoma* (Pisces, Haemulonidae). Zoologica. 33(3): 151–156.

Ginsburg, Isaac. 1950. Review of the Western Atlantic Triglidae (fishes). Texas Jour. Sci. 2(4): 489–527.

Ginsburg, Isaac. 1951. Western Atlantic tongue fishes with descriptions of six new species. Zoologica 36(3): 84–101.

Ginsburg, Isaac. 1952. Eight new fishes from the Gulf coast of the United States, with two new genera and notes on geographic distribution. Jour. Wash. Acad. Sci. 32(3) : 84–101.

Gunter, G. 1945. Studies on marine fishes of Texas. Publ. Inst. Mar. Sci. Univ. Texas 1(1) : 1–190.

Gunter, G. 1948. Notes on fishes of the genus *Scorpaena* from the South Atlantic and Gulf coasts of the United States with descriptions of two new species. Copeia (3) : 157–166.

Gunter, G. 1950. Seasonal population changes and distributions as related to salinity, of certain invertebrates of the Texas coast, including the commercial shrimp. Publ. Inst. Mar. Sci. Univ. Texas. 1(2) : 7–51.

Gunter, G. 1952. Records of fishes from the Gulf of Campeche, Mexico. Copeia (1) : 38–39.

Gunter, G. and H. Hildebrand. 1943. The relation of total rainfall of the state and catch of the marine shrimp *(Penaeus setiferus)* in Texas waters. Bull. Mar. Sci. Gulf & Caribbean. 4(2) : 95–103.

Gunter, G., R. H. Williams, C. C. Davis and F. G. Walton Smith. 1948. Catastrophic mass mortality of marine animals and coincident phytoplankton bloom on the west coast of Florida, November, 1946 to August, 1947. Ecol. Monog. 18: 309–324.

Hedpeth, J. W. 1953. Zoogeography of the Gulf of Mexico. Publ. Inst. Mar. Sci. Univ. Texas 3(1) : 111–224.

Hedgpeth, J. W. 1954. Bottom communities of the Gulf of Mexico, in Gulf of Mexico its origin, waters and marine life. U. S. Fish and Wildlife Service Fishery Bull. 89: 203–214.

Heilprin, Angelo. 1890. The corals and coral reefs of the western waters of the Gulf of Mexico. Proc. Acad. Sci. Philadelphia 42: 303–316.

Higman, J. B. 1952. Preliminary investigation of the live bait shrimp fishery of Florida Bay and the Keys. Fla. Board of Conservation. (mimeo.) : 1–8.

Hildebrand, H. H. 1954. A study of the brown shrimp (*Penaeus aztecus* Ives) grounds in the western Gulf of Mexico. Publ. Inst. Mar. Sci. Univ. Texas 3(2) : 233–366.

Hildebrand, S. F. 1948. A review of the American menhaden, genus *Brevoortia*, with a description of a new species. Smithsonian Misc. Coll. 107(18) : 1–39.

Idyll, C. P. 1950. A new fishery for grooved shrimp in southern Florida. Comm. Fish Rev. 12(3) : 10–16.

Jordan, D .S. and B. W. Evermann. 1898–1900. The fishes of North and Middle America. Bull. U. S. Nat. Mus. 47: 3, 313 pp.

Longley, W. H. and S. F. Hildebrand. 1941. Systematic catalogue of the fishes of Tortugas, Florida. Carnegie Inst. Wash. Publ. 435, Paper Tortugas Laboratory 34: 1–331.

Lowman, S. 1949. Sedimentary facies in Gulf Coast. Amer. Assn. Petrol. Geol. 33(12) : 1939–1997.

Lynch, S. A. 1954. Geology of the Gulf of Mexico, in the Gulf of Mexico, its origin, waters and marine life. U. S. Fish and Wildlife Service, Fishery Bull. 89: 67–86.

Mather, F. S. 1952. Sport fishes o fthe vicinity of the Gulf of Honduras, certain Caribbean Islands and Carmen, Mexico. Proc. of Gulf and Caribbean Fish. Inst. Fourth Annual Session, Miami Beach, November, 1951: 118–129.

Pearse, A. S. 1932. Inhabitants of certain sponges at Dry Tortugas. Carnegie Inst. Wash. Publ. 435, Paper Tortugas Laboratory. 28: 117–124.

Perez–Farfante, Isabel. 1953. Los camarones comerciales de Cuba. Memorias de la Sociedad Cubana de Historia Natural. 21(2) : 1–16.

Perez-Farfante, Isabel. 1954. The discovery of a new shrimp bank at Golfo de Batabano, Cuba. Proc. of Gulf and Caribbean Fish. Inst. Sixth Annual Session, Miami Beach, November, 1953: 97–98.

Pulley, T. E. 1952. An illustrated checklist of the marine mollusks of Texas. Texas Jour. Sci. 4(2) : 167–199.

Rathbun, M. J. 1937. The oxystomatous and allied crabs of America. Bull. U. S. Nat. Mus. 166: 1–278.

Reid, G. K. 1954. An ecological study of Gulf of Mexico fishes in the vicinity of Cedar Key, Florida. Bull. Mar. Sci. Gulf & Caribbean 4(1) : 1–94.

Rivas, L. R. 1951. A preliminary review of the western North Atlantic fishes of the family Scombridae. Bull. Mar. Sci. Gulf & Caribbean. 1(3) : 209–230.

Siebenaler, J. B. 1952. Studies of "trash" caught by shrimp trawlers in Florida. Proc. Gulf & Caribbean Fish. Inst. Fourth Annual Session, Miami Beach, November, 1951: 94–99.

Springer, Stewart. 1950. A revision of North American sharks allied to the genus *Carcharhinus*. Amer. Mus. Novitates. No. 1451: 1–13.

Springer, Stewart and H. R. Bullis. 1952. Exploratory shrimp fishing in the Gulf of Mexico. U. S. Fish and Wildlife Service, Fishery Leaflet 406: 1–34.

Springer, Stewart, and H. R. Bullis. 1954. Exploratory shrimp fishing in the Gulf of Mexico, Summary Report for 1952–1954. Comm. Fish. Rev. 16(10): 1–16.

Teague, G. W. 1951. The sea-robins of America. A revision of the triglid fishes of the genus *Prionotus*. Communicaciones Zool. Museo Hist. Nat. Montevideo 3 (61): 1–58.

APPENDIX

Table A is the station log of drags completed during this investigation. The location of the drags are dead reckoning position; consequently they are not precisely designated. Compass courses are approximated as usually the fishermen follow a fathom contour rather than a definite compass course. The bottom was a fine calcareous sand or mud (coral mud of the fishermen), but sometimes it was mixed with considerable quantities of shells and shell fragments.

Table A

FEBRUARY

Shrimp Trawler "San Jacinto"

Drag No.	Date	Location	Compass Course	Depth	Time	Duration	Remarks
1	2/6/51	NW of Campeche	S	8½	1715–1730	15 m.	Sponge and coral; net snagged
2	2/6/51	NW of Campeche	S	10	1915–2015	1 h.	
3	2/6/51	NW of Campeche	S	10	2030–2230	1 h.	
4	2/6/51	NW of Campeche	S	9	2300–0045	1 h. 45 m.	
5	2/7/51	SW of Campeche	S	10	0050–0245	1 h. 55 m.	Clear
6	2/7/51	SW of Campeche	V	10	0250–0430	1 h. 40 m.	
7	2/7/51	SW of Campeche	S	10	0440–0640	2 h.	
8	2/7/51	SW of Champoton	S	10	1815–2005	1 h. 50 m.	Lots of shell
9	2/9/51	NW of Campeche	S	10	1810–2010	2 h.	
10	2/9/51	W of Campeche	S	10	2025–2210	1 h. 45 m.	
11	2/9/51	W of Pta. Morros	S	10	2230–0010	1 h. 40 m.	
12	2/10/51	SW of Pta. Morros	S	10	0030–0230	2 h.	
13	2/10/51	SW of Pta. Morros	S	10	0240–0430	1 h. 50 m.	
14	2/10/51	NW of Champoton	S	10	1820–2005	1 h. 45 m.	
15	2/10/51	W of Champoton	S	10	2015–2200	1 h. 45 m.	
16	2/10/51	SW of Champoton	S	10	2225–0005	1 h. 40 m.	
17	2/11/51	SW of Champoton	S	10	0015–0200	1 h. 45 m.	Very little trash
18	2/11/51	SW of Champoton	S	10	0215–0400	1 h. 45 m.	
19	2/11/51	SW of Champoton	S	10	0415–0615	2 h.	
20	2/11/51	W of Champoton	S	8	1820–2005	1 h. 45 m.	
21	2/11/51	S.W of Champoion	S	8	2015–2205	1 h. 50 m.	
22	2/11/51	SW of Champoton	S	8	2220–0005	1 h. 45 m.	
23	2/12/51	SW of Champoton	S	8	0020–0200	1 h. 40 m.	
24	2/12/51	SW of Champoton	N	8	0220–0400	1 h. 40 m.	
25	2/12/51	SW of Champoton	N	8	0420–0620	2 h.	
26	2/12/51	SW of Champoton	N	8	1820–2000	1 h. 40 m.	
27	2/12/51	NW of Champoton	N	8	2010–2200	1 h. 50 m.	
28	2/12/51	NW of Champoton	N	8	2215–0000	1 h. 45 m.	
29	2/13/51	NW of Champoton	N	8	0015–0200	1 h. 45 m.	
30	2/13/51	NW of Champoton	S	8	0220–0400	1 h. 40 m.	
31	2/13/51	W of Pta. Morros	S	7	1825–2015	1 h. 50 m.	
32	2/13/51	W of Pta. Morros	S	7	2030–2230	2 h.	
33	2/13/51	W. of Pta. Morros	N	7	2240–0030	1 h. 50 m.	
34	2/14/51	W of Pta. Morros	N	7	0040–0230	1 h. 50 m.	
35	2/14/51	NW of Pta. Morros	N	7	0240–0400	1 h. 20 m.	
36	2/14/51	NW of Pta. Morros	N	7	0410–0610	2 h.	
37	2/14/51	NW of Pta. Morros	N	7	1820–2000	1 h. 40 m.	
38	2/14/51	SW of Campeche	N	7	2045–2245	2 h.	
39	2/14/51	SW of Campeche	N	6	2330–0020	50 m.	
40	2/15/51	NW of Campeche	N	6	0115–0215	1 h.	
41	2/15/51	NW of Campeche	S	8½	0305–0440	1 h. 35 m.	
42	2/15/51	SW of Campeche	S	8½	0500–0620	1 h. 20 m.	
43	2/15/51	SW of Campeche	S	7½	1600–1745	1 h. 45 m.	
44	2/15/51	SW of Campeche	V	7½	1800–1040	1 h. 40 m.	
45	2/15/51	W of Pta. Morros	V	7½	2000–2135	1 h. 35 m.	

Table-A (Continued)

Drag No.	Date	Location	Compass Course	Depth	Time	Duration	Remarks
46	2/15/51	W of Pta. Morros	V	7½	2145–2330	1 h. 45 m.	
47	2/16/51	W of Pta. Morros	V	7½	0700–0715	15 m.	
48	2/16/51	Off of Pta. Morros	V	9	0820–1005	1 h. 45 m.	
49	2/16/51	Off of Pta. Morros	V	9	1020–1220	2 h.	
50	2/16/51	Off of Pta. Morros	V	9	1240–1420	1 h. 40 m.	Lots of sand dollars in net
51	2/16/51	Off of Pta. Morros	V	9	1430–1630	2 h.	
52	2/16/51	Off of Pta. Morros	V	9	1640–1830	1 h. 50 m.	
53	2/16/51	Off of Pta. Morros	V	9	1850–2020	1 h. 30 m.	
Total						88 h.	

JULY

Shrimp Trawler "Texas Clipper"

Drag No.	Date	Location	Compass Course	Depth	Time	Duration	Remarks
1	7/27/51	Off of Campeche	S	16	1855–2100	2 h. 5 m.	
2	7/27/51	Off of Campeche	V	15–16	2120–2330	2 h. 10 m.	
3	7/28/51	Off of Campeche	V	15–15½	2345–0215	2 h. 30 m.	
4	7/28/51	Off of Campeche	V	15–15½	0235–0550	3 h. 15 m.	
5	7/28/51	Off of Campeche	SSW	13	1835–2120	2 h. 45 m.	
6	7/28/51	Off of Campeche	N	13	2140–2350	2 h. 10 m.	Sponges and coral; net snagged
7	7/29/51	Off of Campeche	V	13–14	0210–0510	3 h.	
Total						17 h. 55 m.	

Table B

Table B is the shrimp log of this investigation and all drags were recorded quantitatively. The count is the number of shrimp tails per pound.

FEBRUARY

Shrimp Trawler "San Jacinto"

Drag No.	Weight in pounds headless	Weight in pounds heads on	Count	Remarks
1	Snagged			
2	170	285	20/30	
3	255	425	20/30	
4	340	365	20/30	
5	300	500	20/30	
6	340	565	20/30	
7	255	425	20/30	
8	130	210	15/35	Discarded a few 36/45
9	300	500	20/30	
10	255	425	20/30	
11	255	425	20/30	
12	300	500	20/30	
13	255	425	20/30	
14	170	285	20/30	
15	340	565	20/30	
16	255	425	20/30	
17	255	425	20/30	
18	255	425	20/30	
19	125	210	20/30	
20	550	915	20/35	

Table-B (Continued)

Drag No.	Weight in pounds headless	Weight in pounds heads on	Count	Remarks
21	380	635	20/35	
22	275	460	20/35	
23	255	425	25/35	
24	340	565	20/30	
25	340	565	15/25	
26	360	600	20/30	
27	255	425	20/30	
28	190	315	20/30	
29	210	350	20/30	
30	105	175	20/30	
31	510	850	20/30	
32	425	710	20/30	
33	350	565	20/30	
34	385	640	20/30	
35	300	500	20/30	
36	360	600	20/30	
37	170	285	20/30	
38	85	140	20/30	
39	85	140	20/30	
40	40	65	20/30	
41	170	285	20/30	
42	105	170	20/30	
43	550	915	20/30	
44	170	285	20/30	
45	170	285	20/30	
46	170	285	20/30	
47	Snagged			
48	255	425	20/30	
49	425	710	20/30	
50	380	635	20/30	
51	460	765	20/30	
52	205	340	20/30	
53	180	300	20/30	
Total	13,765	22,910		
		JULY		
		Shrimp Trawler "Texas Clipper"		
1	165	275	15/30	
2	230	385	15/30	
3	285	475	15/30	
4	380	635	15/25	
5	330	550	15/30	
6	190	310	15/30	
7	360	600	15/25	
Total	1,940	3,230		

Studies on the Monogenetic Trematodes of the Texas Coast

I. Results of a survey of marine fishes at Port Aransas, with a review of Monogenea reported from the Gulf of Mexico and notes on euryhalinity, host-specificity, and relationship of the Remora and the Cobia.

By

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INTRODUCTION*

The Monogenea, one of the three orders of the class Trematoda, consists of ectoparasites the majority of which are found on the gills of marine and fresh-water fishes. Several species occur in the mouth and upper respiratory tract of turtles and in the urinary bladder of turtles, frogs and toads. A few have been found on crustacea, particularly on isopods, on copepods, and on *Argulus*. In fishes Monogenea are largely found on the gills and gill chambers and very rarely on the skin and cloaca. This group is not as well known as the digenetic trematodes because they have only slight economic importance. These worms do very little harm to their host; but rarely we find heavy infections and the host may suffer intensely resulting sometimes in death. This is observed mainly in fish-hatcheries, aquaria and similar places where hosts are crowded and kept in artificial containers.

Because of the high degree of host-specificity in this group it is the opinion of the author as well as other workers (Bychowsky, 1933; Hargis, 1953) that the study of this group may throw some light on the phylogenetic relationships of hosts. Therefore, in the systematic study of fishes it will be profitable for ichthyologists to take into consideration the distribution of the monogenetic trematodes on fishes.

No extensive studies have been made before 1952 of the monogenetic trematode fauna of the Gulf of Mexico. A survey of literature shows that only a few species have been described so far from the Gulf. This does not mean that the monogenetic fauna is poorly represented in this part of the world. On the other hand it could reasonably be assumed from the large and varied number of species of fishes occurring in the Gulf that a rich fauna of Monogenea should be similarly represented. Very little is known concerning the occurrence, the distribution, the morphology, the development, or the various relationships of this fauna of the Gulf of Mexico. Bearing these things in mind the author decided to undertake a survey of the monogenetic trematodes from marine fishes of Port Aransas and vicinity. The summer months of June, July, and August of 1952 were spent in field work at the Institute of Marine Science, The University of Texas, Port Aransas, Texas. Over 327 fishes belonging to forty different species were examined at different times. Positive and negative cases were recorded. A note on host-parasite relationship is also included.

MATERIALS AND METHODS

All specimens used in this study were collected by the writer from marine fishes of Port Aransas and vicinity. The summer months attract several hundreds of sports fishermen to this area from all over the country. There are several landing places for fishing boats. These fishing boats bring in their catch not only from the surrounding shallow waters of the bays but also from the waters of the Gulf sometimes forty to fifty miles offshore. The worms studied in this survey were secured from the fish houses and from the sports fishermen.

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* This work was done under the direction of Prof. Sewell H. Hopkins, Department of Biology, A. and M. College of Texas. It is part of a Master's thesis submitted to the Graduate School of the Agricultural and Mechanical College of Texas in August, 1953. Descriptions of the new species of Monogenea reported in this paper are given in the second paper under this series which appears in the same number of this journal.

There is some difficulty in killing trematodes without the body contracting. The method commonly used in this work was to kill the trematodes individually beneath a cover glass on a slide by applying the fixative. When specimens of hosts are available in large numbers it is not possible to examine the gills of all fishes at once, and at such times the writer resorted to freezing as a means of host preservation. The branchial material of these frozen fishes showed that many of the Monogenea present were found to be free from the host tissue. It was found that in addition to the removal action, freezing also has the simultaneous effects of killing the parasites in a relaxed condition free from mucus. Hargis (1953) suggested a new technique by using chloretone for mass collecting. The writer has found this method very satisfactory but was not able to use it in this work.

Gilson's fluid was used as a fixative. Care has to be taken, however, since it has a corrosive effect on the tissues, if left for a comparatively long period of time. After fixation in Gilson's fluid the specimens were transferred to 70% alcohol with sufficient iodine in solution to give it a sherry color, in order to remove the mercuric salts. This solution was changed as frequently as it lost its sherry color and fresh iodine added. The specimens were finally stored in 70% alcohol. The staining and mounting of trematodes after fixation followed well-known techniques. Drawings of individual species were made with the help of a camera lucida and measurements were taken with the aid of a stage micrometer. Curved structures were measured as a straight line extending between the two most distant parts of such structures.

It is difficult to say what kind of fixative will give the most satisfactory results. The use of Bouin's fluid is suggested by Dawes (1946) for Trematoda in general but Mizelle (1939) and Mizelle *et al.* (1944) have found the use of this fixative very unsatisfactory. Instead they had good results with five per cent formalin.

REVIEW OF LITERATURE ON MONOGENEA REPORTED FROM THE GULF REGION

For the present study the author has included under this region areas between latitudes 30° N and 15° N, which embraces the Gulf of Mexico proper, the east coast of Florida, the West Indies, Cuba, Puerto Rico and part of the Caribbean.

A total of thirty species of Monogenea (excluding those reported by the author) have been reported before 1954 from different parts of the Gulf region. Of these, nine species are recorded from Florida, thirteen from Key West and Tortugas, one from Grand Isle, Louisiana, four from the West Indies and the Caribbean, two from Cuba, and one from Puerto Rico.

Most of the early work was done by Linton (1912) and Pratt (1910–1916) at the former Biological Laboratory of the Carnegie Institution at Dry Tortugas, Florida. The species recorded from Tortugas and Key West were collected and described by Linton, Pratt, MacCallum, Brooks, Price, and Fujii. Specific references to these original collections and descriptions are given in the classified list below. Two of the records by MacCallum were not directly from this region but were reported from New York Aquarium from hosts brought from Key West. Fujii (1944) reported five species from Tortugas. The very little that we know of the Monogenea from elasmobranchs of this region comes from the reports of Brooks (1934), who described three new species.

Ten species belonging to the family Dactylogyridae, particularly the subfamily Tetraonchinae, have been reported from the Gulf region; nine of these are from Florida, reported by Mueller (1937), Mizelle and Blatz (1941), Mizelle and Hughes (1938) and Seamster (1938); the single species from Jamaica was reported by Price (1934). Four species of the subfamily Tetraonchinae are reported from the same host-species, *Eupomotis gibbosus,* a fresh-water centrarchid from Florida, which occasionally enters brackish water. Two other species of the same subfamily are reported from two marine fishes which enter fresh water during certain seasons of the year.

Practically no work has been done in this region west of Tortugas, except for a single species reported by Melugin (1940) from Grand Isle, Louisiana.

The following is a classified list of the species recorded from the Gulf before 1954. Manter (1954) in Fishery Bulletin 89 lists only 16 species.

Suborder I. MONOPISTHOCOTYLEA.

Fam. DACTYLOGYRIDAE
Subfam. Tetraonchinae.
Actinocleidus maculatus Mueller, 1937
Host: *Eupomotis gibbosus*—gills. Florida. Reported by Mueller (1937), Seamster (1938), Mizelle & Hughes (1938)
Anchoradiscus anchoradiscus Mizelle, 1941
Host: *Eupomotis gibbosus*—gills. Florida. Reported by Mizelle (1941)
Ancyrocephalus atherinae Price, 1934
Host: *Atherina araea*—Dominican Republic (Samana Bay). Reported by Price (1934)
Cleidodiscus nematocirrus Mueller, 1937
Host: *Eupomotis gibbosus*—gills. Florida. Reported by Mueller (1937)
Rhabdosynochus rhabdosynochus Mizelle & Blatz, 1941
Host: *Centropomus undecimalis*—gills. Florida. Reported by Mizelle and Blatz (1941)
Urocleidus affinis (Mueller, 1937) Mizelle & Hughes, 1938
Host: *Eupomotis gibbosus*—gills. Florida. Reported by Mueller (1937)
Urocleidus spiralis (Mueller, 1937) Mizelle & Hughes, 1938
Host: *Eupomotis gibbosus*—gills. Florida. Reported by Mueller (1937)
Urocleidus hastatus (Mueller, 1936) Mizelle & Hughes, 1938
Host: *Roccus lineatus*—gills. Florida. Reported by Mueller (1936)
Subfam. Diplectaninae
Diplectanum collinsi (Mueller, 1936) Price, 1937
Host: *Roccus lineatus*—gills. Florida. Reported by Mueller (1936)
Neodiplectanum wenningeri Mizelle & Blatz, 1941
Host: *Eucinostomus gula*—gills. Florida. Reported by Mizelle and Blatz (1941)
Fam. UDONELLIDAE
Udonella caligorum Johnston, 1835
Host: Copepod on *Lutinanus griseus*—gills. Tortugas. Reported by Linton (1910)
Fam. MONOCOTYLIDAE
Subfam. Monocotylinae
Heterocotyle floridana (Pratt 1910) Price 1938
Host: *Aetobatus freminvillii*—gills. Tortugas. Reported by Pratt (1910)
Subfam. Dionchinae
Dionchus agassizi Goto 1899
Host: *Echeneis naucrates*—gills. West Indies. Johnson-Smithsonian Deep Sea Expedition. Price (1938)
Dionchus remorae (MacCallum, 1916) Price, 1938
Host: *Caranx hippos* & *Echeneis naucrates*—gills. West Indies. Johnson-Smithsonian Expedition. Price (1938)
Subfam. Loimoinae
Loimosina wilsoni Manter 1944
Host: *Sphyrna zygaena*—gills. Montago Bay, Jamaica. Reported by Manter (1944)

Fam. CAPSALIDAE
Subfam. Capsalinae
Capsala poeyi (Vigueras, 1935) Price 1938
Host: *Makaira ampla*—skin. Havana, Cuba. Reported by Vigueras (1935)
Subfam. Encotyllabinae
Encotyllabe monticelli Vigueras, 1940
Host: *Calamus bajonado*—gills. North coast of Cuba. Reported by Vigueras (1935)
Subfam. Benedeniinae
Entobedella squamula (Heath, 1902) Johnston, 1929
Host. Undetermined fish 'presumably from Gulf of Mexico.' Reported by Price (1939)
Ancyrocotyle bartschi Price, 1934
Host: *Naucrates ductor*—gills. Puerto Rican Deep. Johnston-Smithsonian Deep-Sea Expedition. Reported by Price (1934)
Fam. HEXABOTHRIIDAE
Subfam. Hexabothriidae
Squalonchocotyle ginglymostomae Brooks, 1934
Host: *Ginglymostoma cirratus*—gills. Tortugas. Reported by Brooks (1934)
Squalonchocotyle tiburonis Brooks, 1934
Host: *Sphyrna tiburo*—gills. Tortugas. Reported by Brooks (1934)
Heteronchocotyle hypoprioni Brooks, 1934
Host: *Hypoprion brevirostris*—gills. Tortugas. Reported by Brooks (1934)
Fam. DISCOCOTYLIDAE
Subfam. Vallisiinae
Protomicrocotyle mirabilis (MacCallum, 1918) Johnston & Tiegs, 1922
Host: *Caranx hippos*—gills. Described by MacCallum from New York Aquarium (1918)
Fam. MICROCOTYLIDAE
Subfam. Microcotylinae
Microcotyle incomparabilis MacCallum, 1917
Host: *Caranx crysos*—gills. Key West and New York Aquarium. Reported by MacCallum (1917)
Microcotyloides incisa (Linton 1910) Fujii, 1944
Host: *Lutianus griseus*—gills. Tortugas, Florida. Reported by Linton (1910) & Fujii (1944)
Fam. DICLIDOPHORIDAE
Subfom. Choricotylinae
Choricotyle hysteroncha Fujii, 1944
Hosts: *Bathystoma striatumi, Bachygenys chrysargyreus, Haemulon flavolineatum*—gills. Tortugas. Reported by Fujii (1944)
Choricotyle neomaenis Price 1934
Host: *Lutianus analis*—gills. Key West. Reported by MacCallum (1917)
Heterobothrium affine (Linton, 1898) Price, 1936
Host: *Paralichthys lethostigmus*—gills. Louisiana. Reported by Melugin (1940)
Echinopelma neomaenis (MacCallum, 1917) Raecke, 1945
Host: *Lutianus analis*—gills. Key West. Reported by MacCallum (1917)
Fam. HEXOSTOMATIDAE
Hexostoma macracanthum Fujii, 1944
Host: *Euthynnus alleteratus*—gills. Tortugas. Reported by Fujii (1944)

A NOTE ON EURYHALINITY IN MONOGENEA

Included in this review of Monogenea from the Gulf region are five species belonging to the family Dactylogyridae, whose single host *Eupomotis gibbosus* (fam. Centrarchidae) is a fresh water fish from Florida which is said to enter brackish water (Breder, 1948). These worms are *Actinocleidus maculatus* Mueller, 1937, *Anchoradiscus anchoradiscus* Mizelle, 1941, *Cleidodiscus nematocirrus* Mueller, 1937, *Urocleidus affinis* (Mueller, 1937) Mizelle & Hughes, 1938, and *Urocleidus spiralis* (Mueller, 1937) Mizelle & Hughes, 1938. On the other hand, three other species reported from Florida and belonging to the same family Dactylogyridae were collected from two marine fishes which can enter fresh water during certain seasons of the year. One of these hosts is *Roccus lineatus* (fam. Serranidae), which "ascends rivers, or at least enters bays for the purpose of spawning" beginning in May (Breder, 1948). From this host *Urocleidus hastatus* (Mueller, 1936), Mizelle & Hughes, 1938, and *Diplectanum collinsi* (Mueller, 1936) Price, 1937, were reported. The other host, *Centropomus undecimalis* (fam. Centropomidae), sometimes enters fresh water (Gunter, 1942). From this host only one species has been reported, *Rhabdosynochus rhabdosynochus* Mizelle & Blatz, 1941.

It was stated by Ward (1908) that "the parasitic fauna is primarily a function of the habit of the species" and that marine fishes such as the salmon "carry their marine parasites with them into fresh water but soon lose them." We have no experimental data to prove this statement. On the other hand there is the unique example of two species of *Microcotyle (M. eriensis, M. spinicirrus)* occurring on *Aplodinotus grunniens*, a member of the marine family Sciaenidae, which is found in fresh water. All the other known *Microcotyle* spp. are reported from marine fishes in a marine environment. The single report of *M. eriensis* was by Bangham & Hunter (1936) from Lake Erie. *M. spinicirrus* was first reported by MacCallum (1918) from the same host at the New York Aquarium. Later on it was reported from lower Tallahatchie River by Simer (1929), from Lake Erie by Bangham and Hunter (1936), from Fairport, Iowa by Linton (1940), and from Reelfoot Lake, Tennessee by Bangham and Venard (1942), all from the same host.

In his short discussion on the ecology of Monogenea, Baer (1951, page 124) notes:

> "It is interesting to observe that not a single species of monogentic trematodes has ever been reported from marine turtles. Fresh-water turtles were already separated from the marine species in Mesozoic times and consequently may have acquired their parasites at that period. It is particularly interesting to discover that distinctive fresh-water fishes of Australia harbor an extremely great number of species and genera. These nearly all occur on fishes that have immigrated from the sea at a comparatively recent period (Johnston and Tiegs). In the northern hemisphere, the presence of genera such as *Discocotyle* and *Mazocraes* that are evidently marine on migratory salmonids and on migrating fresh-water herrings shows clearly that these parasites possess a marked degree of euryhalinity."

HOST SPECIFICITY IN MONOGENEA AND A NOTE ON THE PHYLOGENY OF THEIR HOSTS

Host specificity

Investigations by several workers including the author (Bychowsky, 1933; Mizelle *et al.*, 1943; Nigrelli, 1937; Jahn & Kuhn, 1932; Hargis, 1953) on the host-parasite relationships reveal that there is a marked host specificity in most Monogenea. This is attributed to the unusual conditions for isolation which exists in the group such as the absence of a multi-host life cycle together with the device for attaching eggs to the host. Under certain conditions this host-specificity may be less marked, as in a restricted environment like an aquarium, where there is possibility of the fishes exchanging parasites. But even under these abnormal conditions, experiments reveal that there seem to be certain physiological barriers restricting them to species of fishes within a certain genus, subfamily, or family. Thus there are distinct species, genus, subfamily or family specificities exhibited by these parasitic worms.

The investigations of Jahn & Kuhn (1932) conducted at the New York Aquarium were along these lines. They worked on the host specificity of *Benedenia melleni* and prepared lists of fishes which are susceptible and not susceptible to the attack of this parasite. Nigrelli and Breder (1934) continued this work and added some more fishes to the original list. In spite of this restricted environment, all susceptible fishes used in the experiment belong to the order Perciformes (Acanthopterygii). Of this order a high susceptibility is shown by members of the families Serranidae, Lutianidae and Ephippidae, and no infections have been observed in the families Sparidae, Pomocentridae, Echeneidae, and Batrachoididae. It should also be noted, that Jahn & Kuhn exposed six elasmobranchs representing six different families and none was ever observed to be infected. This investigation shows that even within the confines of an aquarium there is a distinct specificity which is above the familial level but below the ordinal.

Recent experiments of Hargis (1953) on host specificity of Monogenea among some fresh-water fishes should be mentioned. He considered the host-parasite relations of twenty-four identified species of Monogenea recovered from fishes of three families from Westhampton Lake, Richmond, Virginia. In his paper Hargis concludes:

> ". . . that a fairly high degree of host-specificity exists among the monogenetic trematodes studied. The work of other authors on the same species supports this conclusion. Even those that occur on more than one host species are, with the exception of *Dactylogyrus aureus*, confined to a subfamily or, at most, a family. The occurrence of *D. aureus* on a fish which is not a species of its normal host family, Cyprinidae, was probably accidental.
>
> "Indeed, the specificity as reported herein and elsewhere (Mizelle, LaGrave and O'Shaughnessy, 1943) is so marked that it is possible to make a fairly accurate identification of the hosts studied above by an analysis of the ectoparasite fauna of the branchial material, provided sufficient material is checked.
>
> "With this degree of host-specificity existing in the Monogenea it is probable that more extensive study of them, especially their life-history, physiology and ecology, with the aim of better understanding the natural taxonomy and phylogeny of both the hosts and parasites will prove profitable."

Phylogeny of hosts

Bychowsky (1933) was the first to point out the significance of the monogenetic trematodes in the investigation of the systematic relationships of cyprinoid fishes. In his classical study he tried to show how information on the distribution of the monogenetic trematodes *Dactylogyrus spp.* could be used for the systematic study of some species of carps. The genus *Dactylogyrus* is generally confined to fresh water cyprinids, several species having been reported. The species of *Dactylogyrus* show both a high and low specificity. In the cases of high degree of specificity the *Dactylogyrus* species are confined to specific cyprinoid fishes, and in the cases of a low degree of specificity a single species of *Dactylogyrus* is found on two different species of hosts, belonging either to the same genus or to closely related genera, that are able to form hybrids. Based on the parasitological evidence he discusses the relationship of *Abramis brama, A. ballerus,* and *A. salpa* which are treated under a single genus by some ichthyologists while others hold the view that they belong to different genera. Berg has stated that hybrids are never formed between these three species of *Abramis.* This Bychowsky says, is in agreement with the parasitological findings. Based on these two lines of evidence

Bychowsky assumes that *A. brama*, *A. ballerus*, and *A. salpa* "are rather sharply separated from each other which is to a certain extent in harmony with the statement of Kasansky" and he adds, "we leave it to the ichthyologists, to decide to which genus or subgenus these species belong." He concludes his paper with the following remark:

> "On the basis of these described examples we have tried to show how the information concerning the distribution of the species of *Dactylogyrus* could be used for the systematics of the carps. It can be seen from these examples, that the modern systematics is not limited to only morphological methods, but instead strive to include the individual taxonomic groups in their biological specialization. The ichthyologists cannot fail to consider also the parasitological findings, namely the statements about the distribution of the monogenetic trematodes. We assume, for example, that the latter could play an important role in the investigation of the phylogenetic relationships of the individual species of the genus *Barbus* which is very rich in species. Further, their importance in the hybridization experiments should be mentioned. With the help of this information it is possible to predict when the most successful results in hybridization can be achieved."

Relationship of the Remora and the Cobia

In confirmation of Bychowsky's hypothesis about the usefulness of knowledge of host distribution of Monogenea in systematic studies of fishes, the author wishes to outline one of his findings along these lines. It deals with the probable phylogenetic relationship of the families of fishes Echeneidae (shark suckers), Rachycentridae (cobias) and Carangidae (jacks). A survey of literature shows different views expressed by ichthyologists at different times. Following is a classification of these fishes based on Berg (1947) which is also accepted by Schultz and Stern (1948).

Order 102 PERCIFORMES (Berg, page 472)
  Suborder *Percoidei*—Perch like fishes.
    Superfam. *Percoidae.* (fifty-nine families, nos. 400–458).
      Fam. 419. *Pomatomidae.* Widely distributed. Single species *Pomatomus saltatrix* (Blue fish).
      Fam. 420. *Scombropidae.* Indo-Pacific and Atlantic.
      Fam. 421. *Rachycentridae.* Pelagic, Atlantic, Indo-Pacific. Single species *Rachycentron canadus* (cobias).
      Fam. 442. *Carangidate.* Widely distributed, largely oceanic fishes e.g., *Caranx hippos* (common jack).
  Suborder *Blennioidei*—Blennioid (Berg, page 479).
      Fam. 494. *Blenniidae*—Blennies.
  Suborder *Scombroidei*—Mackerel-like fishes (Berg, page 483).
    Superfam. *Scombroidae*
      Fam. 525. *Scombridae*—Mackerels—Oceanic fishes.
  Suborder *Gobioidei*—Gobies (Berg, page 486).
  Superfam. *Gobioidae*
      Fam. 541. *Gobiidae.*
Order 109. ECHENEIFORMES (Discocephali)—remoras. As Perciformes, but the spinous dorsal transformed into an adhesive disc placed on the head. Otolith of percid type. (Berg, page 495.)
      Fam. 575. *Opisthomyzonidae*—extinct. *Opisthomyzon.* Vertebrae 23 or 24. Upper Eocene of Switzerland.
      Fam. 576. *Echeneidae*—All warm seas. Vertebrae 26–30. *e.g.*, *Echeneis naucrates* (Shark Remora), *Remoropsis brachyptera* (Swordfish Remora).

The relationship of Discocephali and Rachycentridae is very much in doubt. Gill discussed this point and stated that these two groups are not related. (See, Gill, *in* Jordan & Evermann Bull.U.S.Nat.Mus.Xlvii pp. 2265–2268, 1898.) According to Gill Cuvier's 'Scomberoid' group was split by Günther creating the families Scombridae, with more than 24 vertebrae and Carangidae, with only 24 vertebrae. Since *Rachycentron* has 25 vertebrae it was severed from the free-spined Carangidae and associated with the Scombridae. *Rachycentron* was thought to be closely related to *Echeneis* by Cuvier because "it has an elongate body, flattened head, and a longitudinal lateral band"; therefore *Echeneis* was considered to be next allied to *Rachycentron* and to belong to the same family. Gill was rather emphatic in stating that ". . . in a logical system it *(Echeneis)* must be removed far from Scombridae and probably be endowed with subordinal distinction. In all essential respects it departs greatly from the type of structure manifested in the Scombridae and rather approximates but very distantly the Gobioidea and Blennioidea." This is, according to Gill, because in the gobies and blennies, "there is a tendency of the flattening of the head, of anterior development of the dorsal fin, a simple basis cranii, etc. Nevertheless there is no close affinity, or even tendency to the extreme modification of the spinous dorsal exhibited by *Echeneis.*" In concluding his remarks Gill states: "Whatever may be the closest relations of *Echeneis,* or the systematic value of its peculiarities, it is certain that it is not allied to *Rachycentron* any more than to hosts of Scombroid, percoid, and kindred fishes and that it differs in toto from it notwithstanding the claims that have been made otherwise. It is true that there is a striking resemblance, especially between the young—almost as great, for example, as that between the placental mouse and the marsupial *Antechinomys*—but the likeness is entirely superficial, and the scientific ichthyologist should be no more misled than would be the scientific therologist by the likeness of the marsupial and placental mammals."

Jordan also maintained the same view as Gill's. In his "Study of Fishes" (1905), he placed Discocephali as a suborder "next to the gobies for want of a better place." In this group of fishes the first dorsal fin is transformed into a peculiar laminating disc, which covers the whole top of the head and nape. "In other respects," Jordan states, "the structure does not diverge very widely from the percoid type, there being a remarkable resemblance in external characters to the Scombroid genus *Rachycentron* but the skeleton shows no special affinity to *Rachycentron* or to any perciform fish. The basis of the cranium is simple and in the depression of the head with associated modifications the Discocephali approach the Gobies and Blennies rather than the mackerel like forms." The paleontologist Woodward refers the order Echeneiformes to the Scombridae, as stated by Berg. But Regan (1912) states that the Discocephali differ from the percoids "especially in the remarkable transformation of the spinous dorsal fin into a flat, oval, transversely laminated, adhesive disc, which extends forward on the upper surface of the head. . . . The other fins are very similar to those of the Pomatomidae, Carangidae, Rachycentridae, etc., in structure, and position, and the Discocephali may well have evolved from percoids of this type."

Speaking about the relationship of the Remoras, Breder (1948) has the following view: "The larval development of this form is unknown and until such a time when it is we will likely be in the dark concerning the structural origin of this disc. These fishes bear certain resemblance to the Cobia and it has been suggested that they are related to it." Now speaking about the Cobias (Rachycentridae), Breder (1948) states "In its youth the Cobia bears a striking resemblance to the shark sucker and it has been suggested that they may be related but of this we are not certain at the present time."

Bearing these views of the ichthyologists in mind let us take a look at the parasitological findings. During the course of investigations of the Monogenea of Port Aransas, the author came across a new species of this parasite, *Dionchus hopkinsi* (n. sp.),* occurring on *Rachycentron canadus*. This new species closely resembles *Dionchus agassizi* Goto, 1899, reported from *Remoropsis brachyptera* and *Echeneis naucrates*, both belonging to the fish family *Echeneidae*. The only diagnostic difference was the larger size of the hooks of the opisthaptor in *D. hopkinsi*, n. sp. (also the worm is slightly larger in size than *D. agassizi*, with differences in body proportions). *D. agassizi* was first reported by Goto from *Remoropsis brachyptera* from Newport, Rhode Island. Price (1938) reported the same form from the same host from Woods Hole and New York Aquarium. Price (1938) again reported this from *Echeneis naucrates* from West Indies (collected by Johnson-Smithsonian Deep Sea Expedition). The only other species of the genus *Dionchus* reported so far is *D. remorae* (MacCallum, 1916; Price, 1938), several of which were collected by MacCallum from *Echeneis naucrates* at the New York Aquarium and one specimen from *Caranx hippos*. Price (1938) also reports that several immature specimens of *D. remorae* were collected in 1933 from two specimens of *Echeneis naucrates* taken in West Indian waters by the Johnson-Smithsonian Deep Sea Expedition. It should also be pointed out here that the subfamily Dionchinae is tentatively placed in the family Monocotylidae since its exact position is unknown. The whole subfamily seems to be an aberrant group, possibly indicating a long period of isolated phylogeny.

From the evidence pointed out above it seems that the families Echeneidae and Rachycentridae may be closely related, and probably the former group does not deserve the rank of a separate order but should be reduced to the rank of a family and placed close to the family Rachycentridae under the suborder Percoidei and Order Perciformes. However, it is left to the experienced ichthyologist to decide these relationships, but in making his decisions he should not ignore the parasitological findings. It is also important to state that no other monogenetic trematodes have so far been recorded from the two families Rachycentridae and Echeneidae, which also indicates that both the hosts and the parasites are isolated groups. The fact that one specimen of *D. remorae* was found on *Caranx hippos* indicates some affinity of the family Carangidae to the other two families Rachycentridae and Echeneidae, but this parasitological evidence is not too reliable because the report is not from natural waters but from the New York Aquarium.

Metcalf (1929, 1940) was very enthusiastic over the "Von Ihring Method" to show the paleobiological significance of the distribution of certain parasites and probably went too far in his speculations, but the importance of this method cannot be ignored. This method has been applied by entomologists in the study of such ectoparasites as Mallophaga on birds (Kellogg, 1913; Harrison, 1914; Hopkins, 1942), and Anoplura of mammals (Ewing, 1926). It has also been applied by several protozoologists and helminthologists such as Kirby (1937) on flagellate protozoa of termites, Baer (1948) and Fuhrmann on cestodes of birds, Dougherty (1949) on the metastrongylidae of some marine mammals, Metcalf (1929, 1940) on opalinid protozoa of frogs. The author is inclined towards some of the views expressed by Eichler in his article "Some Rules in Ectoparasitism" (Annals and Magazines of Natural History, Aug. 1948), but one should be extremely cautious because of complications arising from secondary acquisition of parasites from a new region and by their subsequent convergent or divergent evolution. It is also important to emphasize the need for reliable host identification, preferably by a specialist.

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* A full description of this new species appears in the second series of this paper elsewhere in this journal.

RESULTS OF SURVEY

The results of this survey are given in five tables under the following headings:—

1. Host-parasite record.
2. List of fishes negative for Monogenea. (Some of the negative cases reported may have little significance since only a few hosts were examined.)
3. Results of survey at Port Aransas.
4. Host-parasite relationship.
5. Systematic list of Monogenea collected at Port Aransas.

TABLE I

Host-Parasite Record

Scientific and popular name of host	Name of parasite with family	Number of hosts examined	Number of positive cases	Number of negative cases	Total number of parasites
Brevoortia gunteri Menhaden	*Diclidophora lintoni* n.sp. Diclidophoridae	1	1	0	2
Caranx hippos Common Jack	*Pyragraphorus incomparabilis* n.comb. Microcotylidae	10*	2	8*	10
Caranx hippos Common Jack	*Protomicrocotyle mirabilis* Discocotylidae	10*	1	9*	1
Carcharhinus limbatus Spot-fin Ground Shark	*Loimos scoliodoni* Monocotylidae	6	1	5	1
Leiostomus xanthurus Spot	*Diclidophora caudalis* n.sp. Diclidophoridae	1	1	0	1
Mugil cephalus Striped Mullet	*Metamicrocotyla macracantha* n.comb. Microcotylidae	22	1	21	2
Pomatomus saltatrix Bluefish	*Microcotyle pomatomi* Microcotylidae	6	1	5	3
Rachycentron canadus Ling	*Dionchus hopkinsi* n.sp. Monocotylidae	9	5	4	8
Sarda sarda Common Bonito	*Hexostoma pricei* n.sp. Hexostomatidae	10	2	8	4
Scoliodon terrae-novae Sharp-nosed Shark	*Loimos scoliodoni* Monocotylidae	2	2	0	6
Scomberomorus maculatus Spanish Mackerel	*Microcotyle scomberomori* n.sp. Microcotylidae	40†	--	--	7
Scomberomorus maculatus Spanish Mackerel	*Pseudaxine texana* n.sp. Microcotylidae	40†	1	39	1
Scomberomorus maculatus Spanish Mackerel	*Heteraxine scomberomori* n.sp. Microcotylidae	40†	--	--	5
Scorpena plumieri Scorpionfish	*Encotyllabe pricei* n.sp. Capsalidae	2	1	1	1
Sphyrna tiburo Bonnet-head Shark	*Squalonchocotyle tiburonis* Hexabothriidae	4	2	2	7
Cynoscion nebulosus Speckled Trout	All specimens spoiled by improper fixation	26	8	18	17
Cynoscion arenarius Sand Trout		2	1	1	1
Chloroscombrus chrysurus Bumper		3	1	2	1
Sciaenops ocellatus Channel Bass		16	2	14	3

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* Ten Common Jack examined, of which 8 had no *Pyragraphorus* and 9 had no *Protomicrocotyle*.

† Forty Spanish Mackerel examined; the number positive and the number negative for each species of parasite were not recorded separately because the parasites were not identified as different species at the time of collection.

TABLE II

List of Fishes Negative for Monogenea

Scientific name	Popular name	Number of hosts
Archosargus probatocephalus	Sheepshead	1
Asteroscopus y-graecum	Stargazer	3
Bagre marina	Gaff-topsail catfish	15
'Congrid' eel	Eel	2
Coryphaena hippurus	Dolphin	10
Conodon nobilis	Barred-grunt	6
Elops saurus	Tenpounder	10
Galeichthys felis	Sea catfish	25
Istiophorus americanus	Sailfish	12
Lagodon rhomboides	Pinfish	20
Lutjanus blackfordi	Red snapper	10
Micropogon undulatus	Croaker	7
Nautopaedium porosissimum	Midshipman	3
Opsanus tau	Toadfish	2
Paralichthys lethostigma	Flounder	3
Pogonias cromis	Seadrum	4
Promicrops itaiara	Jewfish	1
Remora from Sailfish	Remora	3
Sphyraena spp.	Barracuda	1
Synodus foetens	Lizardfish	6
Tarpon atlanticus	Tarpon	10
Trachinotus carolinensis	Pompano	4
Trichiurus lepturus	Ribbonfish	9
	Total	167

TABLE III

Result of Survey of Monogenea at Port Aransas

Number of fishes examined	327
Number of fishes positive	33
Per cent of fishes infested	10
Number of species of fishes examined	40
Number of species of fishes positive	16
Per cent of species of fishes infested by Monogenea	40
*Number of species of Monogenea recorded	14
Number of genera represented	12
Number of subfamilies represented	7
Number of families represented	7

* Eight new species reported elsewhere in this journal.

TABLE IV

Host-Parasite Relationship

1. *Species of Monogenea attacking two hosts*

Parasite	Host
Loimos scoliodoni (Monocotylidae)	1. *Scoliodon terra-novae* (Sharp-nosed Shark) 2. *Carcharhinus limbatus* (Spot-fin Ground Shark)

2. *Species of hosts infested by more than one species of Monogenea*

Host	Parasite
Caranx hippos (Common Jack)	1. *Pyragraphorus incomparabilis* (Microcotylidae) 2. *Protomicrocotyle mirabilis* (Discocotylidae)

3. *Host species bearing largest number of species of Monogenea*

Host	Parasite
Scomberomorus maculatus (Spanish Mackerel)	1. *Microcotyle scomberomori* (Microcotylidae) 2. *Pseudaxine texana* (Microcotylidae) 3. *Heteraxine scomberomori* (Microcotylidae)

TABLE V

Systematic List of Monogenea Collected at Port Aransas

- SUBORDER MONOPISTHOCOTYLEA
  - I. MONOCOTYLIDAE
    - Dionchinae
      - 1. *Dionchus hopkinsi* n.sp.
    - Loimoinae
      - 2. *Loimos scoliodoni* Manter, 1944.
  - II. CAPSALIDAE
    - Encotyllabinae
      - 3. *Encotyllabe pricei* n.sp.
- SUBORDER POLYOPISTHOCOTYLEA
  - III. HEXABOTHRIIDAE
    - Hexabothriinae
      - 4. *Squalonchocotyle tiburonis* Brooks, 1934.
  - IV. DISCOCOTYLIDAE
    - Vallisiinae
      - 5. *Protomicrocotyle mirabilis* Johnston & Tiegs, 1922.
  - V. MICROCOTYLIDAE
    - Microcotylinae
      - 6. *Pyragraphorus incomparabilis* (MacCallum, 1917) n.comb.
      - 7. *Metamicrocotylea macracantha* (Alexander, 1954) n.comb.
      - 8. *Microcotyle pomatomi* Goto, 1899
      - 9. *Microcotyle scomberomori* n.sp.
      - 10. *Heteraxine scomberomori* n.sp.
      - 11. *Pseudaxine texana* n.sp.
  - VI. DICLIDOPHORIDAE
    - Diclidophorinae
      - 12. *Diclidophora lintoni* n.sp.
      - 13. *Diclidophora caudalis* n.sp.
  - VII. HEXOSTOMATIDAE
    - 14. *Hexostoma pricei* n.sp.

SUMMARY

1. The literature on the thirty species of Monogenea reported from the Gulf region before 1954 is reviewed.
2. A note on euryhalinity in Monogenea is included.
3. A brief review on host specificity in Monogenea and the importance of this knowledge in the systematic studies of fishes is emphasized.
4. The work of Bychowsky (1933) is reviewed to point out the significance of the distribution of Monogenea on different carps in the study of systematic relationships of cyprinoid fishes.
5. The literature on the relationships of the fish families Echeneidae and Rachycentridae is reviewed. Parasitological findings are recorded to show the probable relationship of these two families.
6. A survey is made of the Monogenea on marine fishes of Port Aransas, Texas. Three hundred and twenty-seven fishes belonging to forty different species were examined. The number of positive and negative cases of infestation are recorded, along with data on host specificity. Forty per cent of the species of hosts and ten per cent of fishes examined were found to be infested by Monogenea. Fourteen species belonging to seven families and twelve genera are recorded. (Eight new species are reported elsewhere in this journal).

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REFERENCES

Baer, J. G.
1948. Les helminthes, parasites des vertébres. Relations phylogénetiques entre leur évolution et celle de leurs hotes. Conséquences biologiques et medicales. Ann. Franche—Compté et l'Univ. de Bescincon, 15 pp.

——————.
1951. Ecology of Animal Parasites. Univ. Illinois Press. 224 pp.

Bangham, R. V., and Hunter, G. W. III
1936. Studies on fish parasites of Lake Erie. III. *Microcotyle spinicirrus* MacCallum (1918) char. emend. and *M. eriensis* sp. nov. Trans. Amer. Micros. Soc. 55:334–339.

Bangham, R. V., and Venard, C. E.
1942. Studies on parasites of Reelfoot Lake fish. IV. Distribution studies and check list of parasites. J. Tenn. Acad. Sci. 17:22–38.

Berg, L. S.
1947. Classification of fishes both recent and fossil. English and Russian. J. W. Edwards, Ann Arbor, Michigan.

Breder, M. C.
1948. Field Book of Marine Fishes of the Atlantic Coast. G. P. Putnam's Sons, New York.

Brooks, G. L.
1934. Some new ectoparasitic trematodes (Onchocotylinae) from the gills of American sharks. Parasitology 26:259–67.

Bychowsky, B.
1933. Die Bedeutung der monogenetischen Trematoden fuer die Erforschung der systematischen Bezichungen der Karpfenfische. Zool. Anz. 102:243–251.

Dawes, B.
1946. The Trematoda. Cambridge Univ. Press, London, 644 pp.

Dougherty, E. C.
1949. The phylogeny of the nematode family Metastrongylidae Leiper, (1909); A correlation of host and symbiote evolution. Parasitology 39:222–234.

Ewing, H. E.
1926. A revision of the American lice of the genus *Pediculus*, together with a consideration of the significance of their geographical and host distribution. Proc. U. S. Nat. Museum 68 (19):1–30.

Fujii, H.
1944. Three monogenetic trematodes from marine fishes. Jour. Parasit. 30:153–158.

Gill, in Jordan and Evermann.
1898. Bull. U. S. Nat. Mus. xlvii pp. 2265–2268.

Goto, S.
1896. On some ectoparasitic trematodes from the Atlantic Coasts of the U.S.A., Compt. Rend. 3me. Congr. Internat. Zool., Leyden (1895): 351–352.

Gunter, G.
1942. A list of the fishes of the Mainland of North and Middle America recorded from both fresh water and sea water. Amer. Midl. Nat. 20(2):305–326.
1945. Studies on marine fishes of Texas. Pub. Inst. Mar. Sci. I(I):1–190.

Hargis, W. J. Jr.
1953. Monogenetic trematodes of Westhampton Lake fishes. III. Part 2. A discussion of host-specificity. Proc. Helminth. Soc. Wash. 20:98–104.

Harrison, L.
1914. The Mallophaga as a possible clue to bird phylogeny. Australian Zoologist 1(1):7–11.

Hopkins, G. H. E.
1942. The Mallophaga as an aid to the classification of birds. Ibis. 6:94–106.

Jahn, T. L., and Kuhn, L. R.
1932. The life-history of *Epibdella melleni* MacCallum 1927, a monogenetic trematode parasitic on marine fishes. Biol. Bull. Woods Hole, 62:89–111.

Johnston, T. H.
1929. Remarks on the synonymy of certain tristomatid trematode genera. Trans. & Proc. Roy. Soc. S. Australia, 53:71–78.

Johnston, T. H., and Tiegs, O. W.
1922. New gyrodactyloid trematodes from Australian fishes, together with a reclassification of the superfamily Gyrodactyloidae. Proc. Linn. Soc. N.S.W. 47:83–131.

Kellogg, V. L.
1913. Distribution and species-forming of ectoparasites. Am. Naturalist 47:129–158.

Kirby, H., Jr.
1937. Host-parasite relations in the distribution of Protozoa in termites. Univ. Calif. Publs. Zool. 41:189–212.

Linton, E.
1910. Helminth fauna of the Dry Tortugas. II. Trematodes. (*In* Papers Tortugas Lab. 4), Carnegie Inst. Wash. Publ. 133, 11–98.

———.
1940. Trematodes from fishes, mainly from the Woods Hole region, Massachusetts. Proc. U.S. Nat. Mus. 88:1–172.

MacCallum, G. A.
1917. Some new forms of parasitic worms. Zoopathologica, 1:43–75.

———.
1918. Studies on the Polystomidae. Zoopathologica, 1:101–120.

Manter, H. W.
1944. Notes on the trematode subfamily Loimoinae (Monogenea) with a description of a new genus. Jour. Wash. Acad. Sci. 34:86–89.

Melugin, J.
1940. Studies on marine fish trematodes of Louisiana. (Abstr. of thesis.) Abstr. Theses, Louisiana State Univ. (1938–39) Univ. Bull. 32 (new ser. 1) :89.

Metcalf, M. M.
1929. Parasites and the aid they give in problems of taxonomy, geographical distribution, and paleogeography. Smithsonian Inst. Publs. Misc. Collection 81 (8), 36 pp.

———.
1940. Further studies on the opalinid ciliate infusorians and their hosts. Proc. U.S. Nat. Museum 87:465–634.

Mizelle, J. D.
1940. Studies on monogenetic trematodes. II. New species from Tennessee fishes. Trans. Amer. Micr. Soc. 59: 285–289.

Mizelle, J. D., & Blatz, V.
1941. Studies on monogenetic trematodes. VI. Two new dactylogyrid genera from Florida fishes. Amer. Midl. Nat. 26:105–109.

Mizelle, J. D., & Donahue, Sr. M. Angela.
1944. Studies on monogenetic trematodes. XI. Dactylogyridae from Algonquin Park fishes. Amer. Midl. Nat. 31:600–624.

Mizelle, J. D., Hughes, R. C.
1938. The North American fresh-water Tetraonchinae. Amer. Midl. Nat. 20:341–353.

Mueller, J. F.
1936. Studies on North American Gyrodactyloidea. Trans. Amer. Micr. Soc. 55:55–72.

Mueller, J. F.
1937. Further studies on North American Gyrodactyloidea. Amer. Midl. Nat. 18:207–219.

Nigrelli, R. F.
1937. Further studies on the susceptibility and acquired immunity of marine fishes to *Epibdella melleni*, a monogenetic trematode. Zoologica, N.Y. 22:185–192.

Nigrelli, R. F., Breder, C. M., Jr.
1934. The susceptibility and immunity of certain fishes to *Epibdella melleni*, a monogenetic trematode. Jour. Parasit. 20:258–269.

Pérez Vigueras, I.
1935. *Tristomum poeyi* n.sp. (Trematoda), parasito de *Makaira ampla* Pocy (Pisces). Mem. soc. Cuban Hist. Nat. 9:43–44.

Pratt, H. S.
1910. *Monocotyle floridana,* a new monogenetic trematode. Pap. Tortugas Lab. 4 (Carneg. Pub. 133) :1–9.

Price, E. W.
1934. New monogenetic trematodes from marine fishes. Smithson. Misc. Coll. 91:1–3.

———. 1936. North American monogenetic trematodes. Geo. Wash. Univ. Bull. (Summaries of Doctoral Theses, 1934–36) :10–13.

———. 1937. North American monogenetic trematodes. I. The superfamily Gyrodactyloidea. J. Wash. Acad. Sci. 27:114–130, 146–164.

———. 1938. North American Monogenetic Trematodes. II. The families Monocotylidae, Microbothriidae, Acanthocotylidae, and Udonellidae. J. Wash. Acad. Sci. 28:109–126, 183–198.

———. 1939. North American monogenetic trematodes. III. The family Capsalidae. J. Wash. Acad. Sci. 29:63–92.

———. 1943. North American monogenetic trematodes. VI. The family Diclidophoridae (Diclidophoroidea). J. Wash. Acad. Sci. 33:44–54.

Raecke, M. J.
1945. A new genus of monogenetic trematode from Bermuda. Trans. Amer. Micr. Soc. 64:300–305.

Regan, C. T.
1912. The anatomy and classification of the Teleostean fishes of the order Discocephali. Annals of Nat. Hist. Ser. 8, Vol. 10, pp. 634–637.

Seamster, A.
1938. Studies on gill trematodes from Oklahoma fishes. Amer. Midl. Nat. 20:603–612.

Simer, P. H.
1929. Fish trematodes from the lower Tallahatchie River. Amer. Midl. Nat. 11:563–588.

Sproston, N. G.
1946. A synopsis of the monogenetic trematodes. Trans. Zool. Soc. London 25 (4) : 185–600.

Ward, H. B.
1910. Internal parasites of the Sebago Salmon. Bull. Bur. Fish. (1908) 28:1151–1194.

Studies on the Monogenetic Trematodes of the Texas Coast

II. Descriptions of species from marine fishes of Port Aransas[*]

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[*] This work was done under the direction of Professor Sewell H. Hopkins, Department of Biology, A. and M. College of Texas. It is part of a Master's thesis submitted to the Graduate School of the Agricultural and Mechanical College of Texas in August, 1953. Acknowledgments of the present installment are the same as for the first.

INTRODUCTION

This paper is the second of a series on monogenetic trematodes of the Texas Coast. It is the result of a survey conducted during the summer months of June, July, and August of 1952 on 327 marine fishes belonging to forty different species. Some of these were caught by sports fishermen from Port Aransas, others were brought by commercial fishermen several miles away from Port Aransas and from different parts of the coast-line in Texas. The survey work was done from the Institute of Marine Science of The University of Texas, Port Aransas, Texas. Given below are descriptions of fourteen species of monogenea eight of which are new, four were previously described, and two are new combinations of old species. Redescriptions of old species are given because many of the old descriptions are not complete, being based on only one or two specimens, or poorly fixed and stained materials. The taxonomic position of each parasite is indicated before the description. At the end of the description of each parasite there is a short discussion regarding its relationship to closely allied species if any, and the distribution of the species and genus in the Gulf of Mexico, in North America, or elsewhere.

DESCRIPTION OF PARASITES

Suborder MONOPISTHOCOTYLEA

Fam. MONOCOTYLIDAE
    Subfam. DIONCHINAE

1. *Dionchus hopkinsi n.sp.*

Fig. 2, 6

Host. Rachycentron canadus Linnaeus.—"Ling."
Location. Gills.
Distribution. Off Port Aransas, Texas.
Number of specimens. Eight specimens secured from four of nine hosts examined.
Holotype. U.S.N.M. Helm. Coll. No. 54754.

DESCRIPTION: The body is elongate, 5.1 mm long; width across the region of the ovary is 800 μ, at middle part of body is 550 μ, in front of the opisthaptor is 350 μ, and at the "neck" region is 760 μ. The anterior end is triangular, with a constriction (referred to in measurement as "neck") posterior to the level of the pharynx. The anterior end of the body has a distinct thickened margin, 50 μ wide.

A prohaptor is absent, but the broad anterior end has several adhesive glands almost filling the whole space and opening along the margin. The opisthaptor is oblong and sucker-like, 450 μ in width, its longest diameter, and 300 μ in length, its shortest diameter. The exact number of the characteristic marginal areas of the opisthaptor could not be determined but is approximately fourteen. There is a pair of large strongly pointed hooks close to the dorsal surface and facing ventrally. They measure 160 μ long; the basal plate of the hook is 85 μ by 45 μ with a blunt protuberance below the arch of the hook. Marginal hooklets are not visible. A pair of hooklets is clearly visible above the level of the large hooks and very close to the dorsal surface.

The oral aperture is ventral and median and is about 575 μ from anterior end of body. The globular pharynx is about 250 μ in diameter. The esophagus is short. The intestine bifurcates at about 900 μ from the anterior end of the body forming two branches but they do not have any diverticula and appear to unite about 1.2 mm from the posterior end.

Two pairs of eye spots are seen immediately above the pharynx.

The genital aperture is sinistral and near the margin of the body; the genital atrium is large and lies below the level of the pharynx. The testes are two in number, tandem, at a distance of 125 μ from each other; the anterior testis is large, 250 μ long by 15 μ wide; the posterior testis is smaller than the anterior, 175 μ long by 120 μ wide. The ovary is pre-testicular and median and situated at a distance of 1.4 mm from the anterior end of the body. The vitellaria consists of large follicles, which have a characteristic finger-like shape, and extend from slightly posterior to the level of the genital aperture to about the level where the two intestinal caeca join. There is no vagina. The ootype is tubular; its base is surrounded by large unicellular glands.

DISCUSSION.

This species is named in honor of Dr. Sewell H. Hopkins, Professor of Zoology at Texas A. and M. College, under whom the writer was introduced to the field of parasitology. It closely resembles *Dionchus agassizi* (Goto, 1899) but can be easily distinguished from the latter by its larger size, its finger-like vitellaria, its larger pair of hooks, and by differences in body proportions.

Dionchus is the only genus belonging to the subfamily Dionchinae and has only two species so far recorded. Interestingly enough, both species are confined largely to West Indian waters even though one was recorded from Woods Hole. The type species *Dionchus agassizi* was described by Goto in 1899 from *Remora brachyptera (= Remoropsis brachyptera)*. During the years 1915 and 1922 MacCallum collected seven specimens of this type species from *Echeneis naucrates* at the New York Aquarium and at Woods Hole. Price (1938) reports that several additional specimens, mostly immature, were collected in 1933 by the Johnson-Smithsonian Deep Sea Expedition from *Echeneis naucrates* in West Indian waters. The second species, *Dionchus remorae*, was described by MacCallum in 1916 under the name *Acanthodiscus remorae*, but Price (1938) after a careful study of several of MacCallum's specimens assigned it to the genus *Dionchus*. MacCallum's collections were made from *Echeneis naucrates* at the New York Aquarium, with the exception of one specimen from *Caranx hippos*. The Johnson-Smithsonian Deep Sea Expedition is reported to have collected several immature specimens of *Dionchus remorae* from two specimens of *Echeneis naucrates* taken in West Indian waters.

The one described by the writer is the third species of the genus to be recorded from the Gulf of Mexico region and the third from North America.

World Distribution of the Genus. This genus is not world wide in distribution but has only been collected from West Indian waters, Port Aransas, and Woods Hole.

Fam. MONOCOTYLIDAE
Subfam. LOIMINAE

2. *Loimos scoliodoni* Manter, 1944

Fig. 1, 4, 34, 40

Synonym. Tricotyle scoliodoni (Manter, 1938).
Hosts. 1. *Scoliodon terrae-novae.*
2. *Carcharhinus limbatus*—new host record.
Location. Gills.
Distribution. Port Aransas, Texas.
Previous record. Beaufort, North Carolina from *Scoliodon terrae-novae.*
Number of specimens. Six specimens secured from two *S. terrae-novae.* One specimen from six *C. limbatus.*

REDESCRIPTION: The body is elongate, 6.7 mm in length; the width varies from 400 μ in front of the pharynx, to 900 μ in the region of the ovary and 450 μ in front of the opisthaptor. The anterior end of the body has a neck-like region ending bluntly with a lateral lobe on each side.

The prohaptor (fig. 1) consists of two suckers situated inside a prominent depression between the two lateral lobes of the anterior end. Each sucker is 75 μ in diameter, provided with radial muscles, and has a well-defined circular aperture in the center. Manter (1938) in his original description states that "there is some evidence that a knob shaped median portion of the anterior end of the body is protrusible." This was not noticed in any of the specimens that the writer has examined. The opisthaptor (fig. 40) is distinct and is slightly broader than the anterior end of the body, measuring 430 μ long by 200 μ wide. The outer boundary of the opisthaptor consists of a strong ridge of muscles about 50 μ in width enclosing a big depression which is incompletely divided into right and left halves by a slight constriction of the muscular ridge on the dorsal and ventral sides. Apparently these muscular ridges are able to contract and expand, thereby controlling the volume of the two cup-shaped depressions inside which aid in the adhesion of the parasite to the host. Manter has reported the presence of small hooks in the opisthaptor but none of them were located by the writer. These hooks, according to Manter, are easily lost.

The mouth is ventral in position, slightly posterior to the prohaptor, and marked by a semicircular ridge between the two anterior lobes. There is a non-muscular prepharynx leading to a pyriform, muscular pharynx, the latter measuring 325 μ in length by 260 μ in width. The esophagus is extremely short. The bifurcation of the intestine is at about 800 μ from the anterior end of the body. The two caeca do not give rise to branches but end blindly at the posterior end in front of the opisthaptor. The posterior extremity of the right caecum is about 85 μ longer than the left caecum, an important characteristic not pointed out in Manter's description. The excretory vesicles were not visible.

The ovary is fairly large; its outline could not be determined; it is located about 2.2 mm from the anterior end of the body. The uterus is not visible in the specimens studied. The vagina (fig. 4, 34) is very conspicuous in all specimens; it is oval in shape (measuring 250 μ by 150 μ), and is located on the left side about 1 mm. from the anterior end. The wall of the vagina seems to be provided with thick chitinoid material with numerous transverse ridges. There are five testes. The tubular seminal vesicle makes a backward loop adjacent to the anterior part of the right caecum. It then takes a turn anteriorly and enters an elongated oval-shaped cirrus sac measuring 650 μ in length by 250 μ in width. The cirrus is chitinous-like, and measures about 250 μ in length.

DISCUSSION.

The species described above agrees in almost all essential respects with Manter's *L. scoliodoni*, except for the greater length of the body in the former. But this may be a variation due to age. The Port Aransas species is therefore regarded as identical to Manter's species. *L. scoliodoni* was first described by Manter (1938) under a newly created genus and species *Tricotyle scoliodoni* and was assigned to the family Calceostomidae. His description was based on eight specimens secured from the gills of *Scoliodon-terrae-novae* from Beaufort, North Carolina. However, in 1944 he changed the name of the genus to *Loimos* and assigned it to the subfamily Loimoinae under the family Monocotylidae. Loimoinae was created by Price in 1936 for the single member *Loimos salpinggoides* described by MacCallum (1917) from the gills of *Carcharias obscurus* at Woods Hole. Chauhan and Bhalerao (1945) described *Loimos secundus* from the gills of *Scoliodon sorrakowah* from Rangoon and assigned it to the family, Microbothriidae. These two species of *Loimos* seem to be very similar and an examination of the original specimens is necessary to differentiate the two species. The presence or absence of marginal hooklets as diagnostic fatures of species is not always valid since there is a tendency for these hooklets to be lost while the collector is removing the parasites from the host. Both Manter (1944) and Sproston (1946) place the subfamily Loiminae under the family Monocotylidae.

This is the first record of the genus and species from the Gulf of Mexico and a new host record. Two members of this genus are recorded from North America.

World Distribution of Genus. Bay of Bengal, Atlantic coast of North America, and Gulf of Mexico.

Fam. CAPSALIDAE
Subfam. ENCOTYLLABINAE

3. *Encotyllabe pricei n.sp.*

Fig. 25, 37

Host. Scorpaena plumieri—"Scorpionfish."

Location. Gills.

Distribution. Port Aransas, Texas.

Number of specimens. Single specimen secured from one of two hosts examined.

Holotype. U.S.N.M. Helm. Coll. No. 54755.

DESCRIPTION: The body is ellipsoidal, 2.5 mm. long by 700 μ wide in the middle, varying from 450 μ in the anterior region behind the prohaptor to 550 μ in the posterior region, with the lateral margins of the body infolded. Figure 25 shows a ventral view of the anterior region and a ventro-lateral view of the posterior region. The margins of the body are infolded ventrally; these infoldings are clearly seen on the posterior region. The body is bent and shaped like a bow.

The prohaptors are well developed muscular suckers with a diameter of 130 μ each. Each sucker is incompletely surrounded by a pleated membrane; that of the right side is divided into seven parts by radial lines and looks like the petals of a flower. The divisions of this membrane of the left side could not be determined, since they are all folded, but it may have the same number as the right side. The membrane is incomplete on the dorsal aspect. The dorsal view also shows a small incomplete hollow stalk or base, shaped like a narrow ring from which the pleated membrane arises. This ring-shaped stalk surrounds each sucker and is about 55 μ in height from the surface of the body. The opisthaptor is pedunculated, bell-shaped, and about 350 μ long by 225 μ wide, and is surrounded by a delicate marginal membrane. A pair of large hooks about 150 μ long are visible. No small hooks or marginal hooklets were seen. The pedicel seems to be coming out of the groove formed by the infolding margins of body and is 250 μ long by 150 μ wide.

The pharynx is globular, 275 μ in diameter. The remaining part of the alimentary canal could not be determined since it was covered by vitellaria.

A pair of eye spots is visible on the antero-lateral side of the pharynx.

The genital aperture is on the left side of the body at a level with the pharynx. The cirrus pouch is prominent; its anterior part lies on the left bottom of the globular pharynx while its base lies posterior to the pharynx and to the right of the median line. It is about 95 μ wide at its broadest part. There are two testes, which are oval, and 200 μ long by 100 μ wide. The left testis is 50 μ ahead of the right testis. The ovary, 180 μ long by 150 μ wide, is pretesticular and median in position. There is a well developed, very conspicuous shell gland, 145 μ long by 75 μ wide, immediately in front of the ovary. The posterior vaginal aperture could not be ascertained. Vitelline follicles occupy the entire body width from the posterior part of the pharynx to the posterior end of the body.

DISCUSSION.

This species is named in honor of Dr. E. W. Price in recognition of his valuable contribution to our knowledge of Monogenea, particularly that of the North American region. It resembles *Encotyllabe lintonni* Monticelli, 1909, but differs from it in the following: (1) the two testes at different levels, (*i.e.*, the left one is ahead of the right); (2) shorter hook on the opisthaptor, (3) absence of small hooks and marginal hooklets, (4) a narrow ring like stalk for the pleated membrane of the prohaptor, (5) well developed shell gland, (6) globular pharynx, (7) differences in body measurements.

Only one species is reported from the North American region, which is *Encotyllabe lintonii* Monticelli, 1909, from the gills of *Calamus calamus*. This is represented by a single specimen collected by Linton on July 16, 1903 at the Bermuda Biological Station for Research, Flatts, Bermuda. Since Linton's description of this species was incomplete, Monticelli (1908) secured the specimen and redescribed it, naming the species for the collector. Price (1939) has found Monticelli's description inaccurate and has made certain corrections.

The species described in this paper is the first member of the genus to be recorded from the Gulf of Mexico region and the second from the North American region.

World Distribution of the Genus. This genus contains, so far, eight species which are recorded from different parts of the world: Bermuda, Britain, Belgium, Italy, Japan, Australia, and Galapagos Islands.

Suborder. POLYOPISTHOCOTYLEA

Fam. HEXABOTHRIIDAE

Subfam. HEXABOTHRIINAE

4. *Squalonchocotyle tiburonis* Brooks, 1934

Fig. 24, 35, 36

Host. Sphyrna tiburo Linnaeus—"Bonnet-head Shark."
Location. Gills.
Distribution. Port Aransas, Texas.
Previous record. Tortugas, Florida, from same host.
Number of specimens. Seven specimens from 2 of 4 hosts examined.

REDESCRIPTION: The body is elongate, tapering anteriorly toward the terminal oral sucker; the posterior end bears an appendix. The length is 3.2 mm.; the width is 175 μ behind the oral sucker, 550 μ across the region of ovary, and 400 μ in front of the opisthaptor.

The prohaptor consists of a single oral sucker surrounding the mouth and measuring 275 μ transversely and 150 μ vertically. The opisthaptor is oval, 1.05 mm. by 500 μ to 600 μ, and bears six suckers each having a diameter of 200 μ. Each sucker, in addition to having septate walls encircling a comparatively large aperture, bears a hook shaped like the letter "C" and measuring 650 μ in length. Arising from the right anterior side of the opisthaptor is an appendix 750 μ long by 160 μ wide with two oval suckers at its end. Fig. 36 shows the appendix from a worm other than the one shown in fig. 24. The hooks in the appendix are not visible.

The mouth leads into a pharynx (which is not visible in the specimens at hand). The intestinal bifurcation takes place at a distance of 450 μ from the anterior end. Each intestinal caecum gives rise to small diverticula. It is difficult to see the intestinal caeca in the opisthaptor because of the opaque nature of that region.

The ovary is in the middle part of the body and is approximately 300 μ in length. A uterus is seen going forward; at the anterior end of the uterus there is a long single egg, the body of which measures 160 μ by 50 μ. The opening of the genital atrium is not visible. There are numerous testes located behind the ovary for a distance of 600 μ. They are partly covered by vitellaria so that the exact number could not be determined. Due to the presence of vitellaria throughout the body the exact nature of the reproductive ducts is not clear.

DISCUSSION.

This species was first described by Brooks (1934) from the same host at Tortugas, Florida. He also reports that some young specimens were found with the adult which they resembled in size, shape, and angularity of the haptoral sclerites, and that the anchors on the appendix were of the same size. Price (1942) created a new genus *Neoerpocotyle* and placed the above species under the name *N. tiburonis.*

This species is reported for the second time from the Gulf of Mexico. Another member of the genus, *S. ginglymostomae* from *Ginglymostoma cirratum,* was reported by Brooks 1934 from Tortugas, Florida. Thus two members of the genus *Squalonchocotyle* are now reported from the Gulf of Mexico. In addition to these two species from the

Gulf, five other species of the same genus are reported from the Atlantic coast and one species from the Pacific coast.

World Distribution of the Genus. Squalonchocotyle is a genus infesting Squalidae and is world wide in distribution. Species of this genus are reported from the Belgian coast, Ireland, Mediterranean Sea, Adriatic Sea, Morocco, Japan, Australia, Pacific coast of U.S.S.R., and North America.

Fam. DISCOCOTYLIDAE

Subfam. VALLISIINAE

5. *Protomicrocotyle mirabilis* (MacCallum 1918) Johnston and Tiegs, 1922

Fig. 17, 16, 19, 22, 23, 28

Synonym. Acanthodiscus mirabile MacCallum, 1918.
Host. Caranx hippos Linnaeus—"Common Jack."
Location. Gills.
Distribution. Off Port Aransas, Texas.
Previous record. New York Aquarium.
Number of specimens. A single specimen was secured from one of ten hosts examined.

DESCRIPTION: The body is long, slender, 5.4 mm. long by 275 μ wide at the broadest part of the body. The lateral margins of the body are almost parallel. The cuticle at the posterior region of the body shows transverse ridges, the edges of which are directed anteriorly. The width of the body across the prohaptor is 180 μ.

The prohaptor consists of a pair of oval suckers 170 μ long by 50 μ wide, opening into the oral cavity. The opisthaptor is not distinct from the body, has a prominent posterior lobe, and is asymmetrical in having the four suckers only on the right side. The distance from the anterior end of the first sucker to the posterior end of the fourth sucker is 440 μ. The distance from the last sucker to the posterior lobe is 40 μ. The four suckers are clamp-like (fig. 16) and arranged in a single row. There is a prominent Y-shaped transverse groove between the first and second suckers, the two limbs of the "Y" starting from the margin of the body, while the vertical limb of the "Y" ends in a line between the inner margins of the first two suckers. Each sucker is 60 μ long by 50 μ wide. The posterior lobe is 700 μ long by 200 μ wide, and is attached to the main axis in a transverse manner. This lobe shows the presence of hooks; as the lobe was slightly twisted only two of them could be seen clearly, one on each end. Each of these recurved hooks with its broad base is 35 μ long by 20 μ wide at the base (fig. 22). Prominent parallel lines which are very close together are seen traversing the inner surface of the lobe from one end to the other.

The oral aperture is slightly subterminal. The pharynx is oval, 75 μ long by 45 μ wide. The remaining part of the alimentary canal is not visible.

The genital aperature is median. The testis is long and follicular, 1 mm. long by 150 μ wide, and is in front of the ovary. The vas deferens consists of a posterior tortuous portion 200 μ long, and an anterior straight tube 325 μ long ending in a cirrus, 150 μ long by 120 μ wide, with many spines on it (fig. 19). The middle part of the worm under study is slightly damaged immediately behind the region of the testis and hence the anterior part of the ovary is not visible. But the ovary is behind the testis and appears to be long and diffuse. Vitalline follicles are seen extending from behind the region of the vaginal aperture to almost the anterior end of the opisthaptor. The vaginal aperture is dorsal and slightly to the right of the median line, and is a short distance posterior to the level of the genital aperture. It is marked by an oval plate-like mass of spines about 130 μ long by 100 μ wide (fig. 23).

DISCUSSION.

This species was first described by MacCallum in 1918 and was based on eleven specimens representing two collections made by him at the New York Aquarium. In 1936 Price in his Ph.D. thesis re-described this species after a careful study of MacCallum's original specimens, which according to Price "were not in good condition and the majority of them were badly twisted or otherwise distorted," except two which formed the basis of his study. Pointing out the errors in MacCallum's paper, Price states that "the dimensions listed are all erroneous; there are no body spines as reported; there is but one testis instead of 40 or more; and the ovary and testis are in the posterior third of the body instead of in the equatorial third as illustrated." The testis in this species is very long and follicular and is in front of the ovary. The specimen described above is larger than MacCallum's which according to Price is 1.3 to 2.2 mm long by 153 to 340 μ wide while the former is 5.4 mm long by 275 μ wide. Apparently MacCullum's specimens were young worms.

There is considerable difference of opinion as to the systematic position of this unique genus. MacCallum placed it in the family Gyrodactylidae on account of the apparent resemblance of the posterior lobe of the haptor to the haptor of the Gyrodactylids. Johnston and Tiegs (1922) exclude it from the Gyrodactyloidea because of the absence of head organs. But they do not regard this as a true microcotylid and state "that a more accurate study of its anatomy may lead to its falling into a new family." Poche (1926) erected a new family Protomicrocotylidae for its reception, recognizing its close affinities to Microcotylidae. Price (1936) does not give a family status to this group but creates the subfamily Protomicrocotylinae under the family Microcotylidae for its reception. However, Sproston (1946) does not recognize the creation of a separate subfamily for this genus but includes it in the subfamily Vallisiinae under the family Discocotylidae for certain valid reasons. The subfamily Vallisiinae was created by Price in 1943 to include the genus Vallisia on account of its unique type of asymmetrical body and the pre-ovarial testes. This seems to be more appropriate since the testes are pre-ovarial in position even though Price noted it otherwise. The writer agrees with Sproston's 1946 view that:

> "As a matter of convenience and as a temporary measure, until our knowledge of these aberrent forms is increased, it is proposed herein to include *Protomicrocotyle* Johnston and Tiegs in this subfamily (*i.e.*, Vallisiinae), since it is the only other monogenetic genus in which the ovary is wholly posterior to the testes; both genera have the body axis bent at an angle, though in *Protomicrocotyle* this asymmetry is in the posterior quarter of the worm. The structure of the larval haptor and of the region bearing the asymmetrically placed clamps, indicates that this genus is clearly of a different evolutionary line from Vallisia. It is not more closely allied to Microcotylidae, and owing to the limited number of clamps it is perhaps preferable to group it with Discocotylidae—albeit a somewhat heterogeneous assemblage."

A second species of the genus *Protomicrocotyle*, *P. pacifica*, is reported by Meserve (1938) from *Xurel marginatus* from Port Culebra, Costa Rica. A very closely related genus *Lethacotyle* is described by Manter (1953) having only one species, *L. fijiensis*, which is reported from "Yellow Jack" from Fiji Islands. Another related genus is *Bilaterocotyle* Chauhan, 1945 based on a species *(B. chirocentrosus)* from the gills of *Sciaena belengeri* and *Chirocentrua dorab* at Bombay, India.

The species described above is reported for the first time from the Gulf of Mexico region and is the second report for the North American region.

World Distribution of the Genus. There are only two species in this genus, *P. mirabilis* confined to the North American region and *P. pacifica* reported from Pacific coast of Costa Rica.

Fam. MICROCOTYLIDAE

Subfam. MICROCOTYLINAE

6. *Pyragraphorus incomparabilis* (MacCallum, 1917) Comb. nov.

Fig. 12, 15, 45

Synonym: Microcotyle incomparabilis MacCallum, 1917.
Host. Caranx hippos—Common Jack.
Location. Gills.
Distribution. Port Aransas, Texas.
Previous record. New York Aquarium (from Key West, Florida) from *Caranx crysos*.
Number of specimens. Ten specimens secured from two of ten hosts examined.

REDESCRIPTION: The body is long, oval, with a characteristic opisthaptor giving the false appearance of an *Axine* or *Heteraxine*. The length is 4.6 mm, the width 400 μ at the region of the intestinal bifurcation, 900 μ across the region of the ovary, and 325 μ in front of the opisthaptor.

The prohaptor consists of two oval suckers, 75 by 45 μ, adjacent to the pharynx. These suckers are septate with a median aperture in each. The opisthaptor is the most peculiar and misleading structure in the worm. It arises from the narrow end of the body behind the testes and enlarges sideways forming a crescent shaped disc, the outer margin of which measures 3.15 mm and bears 75 to 82 clamps. In some specimens the two rows of clamps are seen side by side, almost overlapping. In others only one row of clamps is seen. Each clamp, measuring 45 μ long by 25 μ wide, is attached by muscles to the disc and seems to be slightly different in structure from the usual Microcotylean type.

The mouth is seen as a small aperture on a level with the anterior end of the prohaptor. The pharynx is comparatively small, 60 μ by 25 μ. There is a distinct esophagus about 100 μ in length. The intestine bifurcates at a distance of 250 μ from the anterior end. Each caecum gives off diverticula from its outer side. The caeca end blindly in front of the opisthaptor and do not enter the latter.

The genital atrium is oval in outline and is immediately behind the intestinal bufurcation. There is a vaginal opening behind this. The ovary is circular with a diameter of 400 μ; the margins form undulations. It is situated at a distance of 1.7 mm from the anterior end of the worm. The uterus is seen going up and opening into the vagina. No eggs were seen. The testes are numerous, arranged behind the ovary and between the two intestinal caeca; their exact number cannot be determined. They do not enter the opisthaptor. The vitellaria are abundant; they extend from the intestinal bifurcation up to the opisthaptor but do not enter the latter even though MacCallum (1917) reports otherwise.

DISCUSSION.

This species was reported by MacCallum (1917) from *Caranx crysos* at the New York Aquarium. The host was brought from Key West, Florida. Meserve (1938) considers this a valid species. However, this seems to belong to the genus *Pyragraphorus* because of the horizontally placed opisthaptor.

This species is recorded for the second time from the Gulf of Mexico, the first report being from a different host.

World Distribution of Species. Gulf of Mexico.

Fam. MICROCOTYLIDAE

Subfam. MICROCOTYLINAE

7. *Metamicrocotyla macracantha* (Alexander, 1954) Comb. nov.

Fig. 26, 31, 41

Synonym: Microcotyle macracantha Alexander, 1954.
Host. Mugil cephalus Linnaeus. "Striped Mullet."
Location. Gills.
Distribution. Port Aransas, Texas, and Coyote Bay, Gulf of California.
Previous record. Gulf of California from *Mugil cephalus.*
Number of specimens. Two specimens secured from one of twenty-two hosts examined.

REDESCRIPTION: The body is slender and elongate; it is 3.5 mm in length; the width is 250 μ at the region of the intestinal bifurcation, 475 μ at the region of the ovary and 650 μ in the middle part of the body. The posterior part of the body in front of the opisthaptor does not taper but has almost the same width as the middle part.

The prohaptor consists of two oval suckers, 42 μ by 25 μ, and provided with radial muscles (fig. 41). Numerous denticles are seen in the cavity of each sucker. The distance between the two suckers is about 5 μ. The opisthaptor (fig. 31, from another worm) is distinct, 750 μ long by 250 μ wide, with a characteristic construction. There is a deeply stained, globular muscular area immediately in front of the opisthaptor. There are about 17 clamps on each side of the opisthaptor; the middle nine clamps of each row are bigger than the others.

The mouth is subterminal; the pharynx is globular and muscular, 30 μ in diameter. There is a distinct esophagus 50 μ in length, at the posterior end of which are numerous esophageal glands. The intestine bifurcates at a distance of 150 μ from the anterior end. Each intestinal caecum gives off diverticula on either side. The right caecum enters the opisthaptor for a distance of 125 μ and ends blindly while the left one proceeds farther for a distance of 500 μ and occupies almost a median position in the opisthaptor.

The ovary is situated at about 900 μ from the anterior end and fills the space between the two intestinal caeca. The testes are numerous, follicular, approximately 40 to 50 in number, and run for a distance of 1.45 mm. (Fig. 26 does not show the exact number of testes.) A highly convoluted thickwalled seminal vesicle is seen starting from the neighborhood of the ovary and ending at the region of the intestinal bifurcation. The genital atrium is small and median ventral and is situated at the point of intestinal bifurcation. The vitellaria are diffuse and are seen as dark spots all over the surface of the body except in the area occupied by the ovary, testes, and seminal vesicles. They enter the opisthaptor for a short distance.

DISCUSSION.

This species is very closely allied to *Microcotyle macracantha* Alexander, 1954. (Alexander's species belongs to the genus *Metamicrocotyla* created by Yamaguti in 1953 for those *Microcotyle* spp. without vagina.) However, the Port Aransas species differs from *M. macracantha* mainly in being smaller in size. In the absence of more specimens for study this Port Aransas species is tentatively assigned to Alexander's species. *Metamicrocotyla bora* Yamaguti, 1953 is also allied to this species but differs mainly in having only a few testes (over a dozen).

Two other species of *Microcotyle* have been described in the past from *Mugil cephalus.* They are *Microcotyle cephalus* Azim, 1939 reported by Azim from Alexandria and *M. mugilis* Vogt, 1878 from Roscoff. These two species need restudy; probably they belong to the genus *Metamicrocotyla.* Yamaguti described another species of *Metamicrocotyla* (*M. filiformis* Yamaguti, 1953) from a single specimen from *Mugil cephalus.* A careful restudy of all the species of Microcotylinae reported from *Mugil cephalus* from different parts of the world might throw some light on the validity of the species of *Mugil* distributed in different oceans.

This is the first member of the genus *Metamicrocotyla* to be reported from the Gulf of Mexico.

World Distribution. Microcotyle infections of mullets have been reported from Genoa, Alexandria, Sea of Araike near Japan, Gulf of California, and Celebes. Some of these reports may refer to species of *Metamicrocotyla.*

Fam. MICROCOTYLIDAE

Subfam. MICROCOTYLINAE

8. *Microcotyle pomatomi* Goto, 1899

Fig. 10, 13, 18, 39

Host. Pomatomus saltatrix Linnaeus—"Bluefish."
Location. Gills.
Distribution. Off Port Aransas.
Previous record. Rhode Island and Woods Hole, from same host.
Number of specimens. Three specimens were secured from one of six hosts examined.

REDESCRIPTION. The body is elongate, tapering gradually towards the ends (fig. 10). The length is 4.5 mm; the width 370 μ at the region of the genital atrium, 500 μ across the region of the ovary, and 350 μ in front of the opisthaptor.

The prohaptor (fig. 39) consists of two circular suckers, each 60 μ in diameter. The opisthaptor (fig. 18, from another worm) is 2.6 mm in length by 300 μ in width at the anterior end, gradually tapering to a point posteriorly. There are two rows of clamps close together; each row consists of 70 clamps; each clamp measures 70 μ long by 20 μ wide.

The pharynx is not visible. There is a long esophagus about 525 μ in length. The intestine bifurcates at a distance of 700 μ from the anterior end. The caeca do not give rise to diverticula, and end blindly at the posterior end.

The genital atrium is situated in front of the intestinal bifurcation (a distinguishing characteristic). It is about 425 μ from the anterior end and has an atrial diameter of 200 μ. Another characteristic is the presence of an unarmed cirrus, 300 μ long by 50 μ wide, on the left side of the genital atrium. The ovary is situated in the middle part of the body about 2 mm. from the anterior end. The testes are numerous; the exact number cannot be determined. Reproductive ducts are not clearly visible.

DISCUSSION.

This species can be distinguished by the genital atrium in front of the intestinal bifurcation, and by the presence of 70 clamps on each side of the opisthaptor. It was first described by Goto (1899) from the same host from Newport, Rhode Island. Later it was reported by MacCallum in 1913 and Linton in 1940 from Woods Hole. Meserve (1938) considers this a valid species.

This is the first report of its occurrence in the Gulf of Mexico.

World Distribution of Species. Atlantic coast of North America and Gulf of Mexico.

Fam. MICROCOTYLIDAE

Subfam. MICROCOTYLINAE

9. *Microcotyle scomberomori* n.sp.

Fig. 11, 7, 48

Host. Scomberomorus maculatus Mitchill—"Spanish Mackerel."
Location. Gills.
Distribution. Off Port Aransas.
Number of specimens. Seven specimens secured from 40 hosts examined.
Holotype. U.S.N.M. Helm. Coll. No. 54756

DESCRIPTION: The body is elongate, tapering towards each end, the posterior one being more pointed. The anterior part forms a head-like portion by a depression on either side. The length of the body is 4.5 mm; the width is 200 μ across the pharyngeal region, 350 μ across the genital atrium, 550 μ across the region of the ovary, and 275 μ in front of the opisthaptor.

The prohaptor (fig. 48) consists of two long oval suckers, 75 μ by 28 μ; the pointed end of each faces the margin of the body instead of the pharynx. Each sucker is septate; the walls are 6 μ in width and encircle a prominent aperture. The opisthaptor is 1 mm. in length; it tapers to a point posteriorly. There are 35 to 40 clamps on each side of the opisthaptor.

The mouth is subterminal. There is an oval pharynx, not very muscular, 55 μ by 32 μ. The esophagus is comparatively long. Intestinal bifurcations and caeca are not visible. The ovary is long, 450 μ in length, and is located 2.2 mm from the anterior end of the body. It appears to be right of the median line. The testes are numerous polygonal bodies. Several of these testes are seen in the same level with the ovary on its left side. The diagnostic features of this species is its characteristic armed cirrus located inside a muscular sac. The cirrus (fig. 7) is about 200 μ long by 35 μ wide with a knob-like anterior end which is provided with spines pointing anteriorly (not shown in the figure). The spines on the main body of the cirrus are longer than those shown in the figure and are arranged like inverted "V" 's. A vagina is seen near the base of the cirrus.

Discussion

This species could be easily identified by the following diagnostic features: (1) characteristic cirrus, (2) anterior neck-like portion with the oval suckers whose pointed ends face anterolaterally, (3) narrow pointed opisthaptor with 35 to 40 clamps, (4) anterior part of testes appearing in the same level with the ovary on its left.

No *Microcotyle* species have been reported from this host anywhere. This is the first record for the Gulf of Mexico and the North American region in general.

GENERAL CONSIDERATIONS ON THE GENUS MICROCOTYLE

1. *Taxonomic Considerations*

Writing about the difficulties and drawbacks in describing new species of the genus *Microcotyle,* Sproston (1946) observes:

> "One of the most difficult genera in Monogenea is *Microcotyle,* which, as it stands in the literature, comprises over seventy species. Some of these are very inadequately described, and in many instances the only reliable difference is the species of host. In the past, far too much confidence has been placed in size-differences and in the number of clamps on the haptor; neither of these factors is of the slightest use unless large numbers of individuals have been compared, extending over a wide growth-range. Remley has contributed a most valuable study of *M. spinicirrus,* in which he has shown that the length of the body can increase more than six-fold during life, and meanwhile new clamps are continually being added to the proximal end of the haptor. He has also shown that a number of characters, hitherto accepted as "permanent," alter during growth, and that egg-size is variable. The present studies confirm the findings of Remley (1936, 1942), and add to the characters which are to be regarded with scepticism when defining a species. Among these are the appearance and relative size of the genital organs, which undergo very great changes during a sex-cycle which is almost as pronounced in some species as it has been shown to be in *Kuhnia scombri.* Most of the *Microcotyle* spp. have been left in this genus until their re-study furnishes sets of characters on which they can be subdivided."

2. *World Distribution of the Genus*

Dawes (1946) observes that at least twenty-two species of *Microcotyle* occur in Japan, about twenty in North America, about seventeen in Europe, six in Australia, and different single species in Egypt, Java, the Galapagos Isles, and the Philippines. Several species have been added since then.

Fam. MICROCOTYLIDAE

Subfam. MICROCOTYLINAE

10. *Heteraxine scomberomori n.sp.*

Fig. 3, 5, 8, 47

Host. Scomberomorus maculatus Mitchill—"Spanish Mackerel."
Location. Gills.
Distribution. Off Port Aransas, Texas.
Number of specimens. Five specimens secured from 40 hosts examined.
Holotype. U. S. N. M. Helm. Coll. No. 54757.

DESCRIPTION: The body is elongate and tapers gradually from the opisthaptor to the anterior end. The length is 6 mm. The width varies, being 350 μ at the region of the genital aperture, 700 μ across the middle part of the ovary, and 900 μ in front of the opisthaptor.

The prohaptor consists of two oval suckers each measuring 75 μ by 35 μ, with radial muscles. Each sucker has an aperture with irregular margins; the aperture seems to lead into a pocket about 15 μ in depth. The opisthaptor consists of a long frill-like, clamp-bearing part of the body which is obliquely and asymmetrically set. The right part of the opisthaptor is 3.8 mm. in length and bears 116 clamps; its anterior end is in the same level with the anterior end of the testes. But the left side is short, about 1.3 mm. in length, and bears only about 45 clamps. Each clamp is 110μ long by 20 μ wide. Longitudinal muscle fibers from the body are seen extending into the region of the clamps.

The mouth is subterminal. The pharynx is 95 μ wide, and is not provided with strong muscles. The esophagus is comparatively long, 35 μ in length. The intestinal caeca are not visible because of the vitellaria.

The genital aperture is median. The ovary starts 2.45 mm from the anterior end of the body, is 1.1 mm. long by 100 μ wide and is situated slightly to the right of the median line. The testes are numerous, approximately 40 to 45 in number. They are found immediately behind the ovary and run for a distance of 1.3 mm in length. The details of the reproductive ducts could not be made out, but there is a prominent median vagina which seems to open dorsally. Its anterior end is circular, 85 μ in diameter, with four or five ridges projecting into the lumen. Numerous spines are seen inside the vaginal tube. This type of vagina is the characteristic feature of the species.

DISCUSSION.

This is the second member of the genus to be reported from the North American region. The first, *Heteraxine carangis* was reported by MacCallum (1918) from the gills of *Caranx hippos* from the New York Aquarium. This is the first record of a *Heteraxine* from the Gulf.

World Distribution. Seven species of the genus *Heteraxine* have been reported from different parts of the world: Japan, East China Sea, Panama, Galapagos Islands, and east coast of North America.

Fam. MICROCOTYLIDAE

Subfam. MICROCOTYLINAE

11. *Pseudaxine texana n.sp.*

Fig. 30, 21, 33, 20

Host. Scomberomorus maculatus Mitchill—"Spanish Mackerel."
Location. Gills.
Distribution. Off Port Aransas, Texas.
Number of specimens. Single specimen from one of 40 hosts examined.
Holotype U. S. N. M. Helm. Coll. No. 54758.

DESCRIPTION: The body is elongate, and is made asymmetrical by the presence of a haptor with clamps only on the left side. There is a neck-like region whose cuticle shows conspicuous transverse ridges. A similar feature was noticed in the posterior end of *Protomicrocotyle mirabilis*. The anterior end of the body is blunt and broad, measuring 180 μ in width; its anterior margin is almost perpendicular to the longitudinal axis of the body. The length of the body is 2.38 mm; the width is 225 μ at the "neck" region, 500 μ across the region of the ovary, and 400 μ in front of the anterior end of the opisthaptor.

The prohaptor (fig. 21) consists of two oval suckers, 72 μ by 40 μ, which are provided with radial muscles and papilla-like projections without any aperture in the center. The opisthaptor is oblique and unilateral; it bears approximately 45 clamps, the most anterior part of which is coiled inwards and is in line with the testes. Each clamp is oval in shape and measures 50 μ by 35 μ (fig. 33). The posterior end of the opisthaptor has an area free from clamps measuring 150 μ in length, but it bears a pair of anchors at its posterior end; each anchor is 30 μ in length and has two roots (fig. 20).

The mouth is terminal and appears as a depression in the center of the flat anterior end. The pharynx and esophagus are not visible. The intestinal bifurcation is at a distance of 250 μ from the anterior end. The intestinal caeca are hidden by vitellaria in the main part of the body but become very clear as they enter the opisthaptor where the two caeca unite at a distance of 300 μ from the posterior end, and do not proceed beyond that region.

The details of the reproductive system, particularly the ducts, are not visible because of the thickness of the worm. The ovary is situated in the middle region of the body at a distance of 850 μ from the anterior end. Its outline is not clear. There is a series of testes, approximately 50 to 60, arranged below the ovary for a distance of 700 μ. The genital pore seems to be near the region of the phaynx. Vitellaria are found throughout the body, except the opisthaptor and the anterior region above the pharynx.

DISCUSSION.

This species is probably closely related to *P. mexicana* Meserve, 1938, secured from the same host at Tangola-Tangola, Pacific coast of Mexico. However it differs from it in several aspects. The following are the identifying features of this species: (1) blunt anterior end whose outline is almost horizontal measuring 180 μ in length; (2) conspicuous transverse striations or ridges at the anterior part of the body; (3) presence of 45 clamps; (4) only one pair of anchors on the opisthaptor; (5) caeca unite in the opisthaptor.

This is the first record of a *Pseudaxine* species for the Gulf of Mexico and Atlantic regions.

World Distribution of Genus. Five species of *Pseudaxine* have been reported by various workers from different parts of the world. One species occurs in the Mediterranean (Genoa), one in the Arabian Sea (Bombay), two in Japan and one species on the Pacific coast of Mexico.

Fam. DICLIDOPHORIDAE

Subfam. DICLIDOPHORINAE

12. *Diclidophora lintoni n.sp.*

Fig. 27, 32, 42, 44, 49

Host. Brevoortia gunteri—"Menhaden."
Location. Gills.
Distribution. Port Aransas.
Number of specimens. Two specimens secured from one host.
Holotype. U. S. N. M. Helm. Coll. No. 54759.

DESCRIPTION: The body is elliptical, 2.84 mm. long by 750 μ wide at level of ovary. The anterior haptor is in the form of a pair of suckers, 25 μ in diameter, opening into the oral cavity (fig. 44). The posterior haptor is rectangular, 400 μ long by 550 μ wide, and is slightly set off from the body proper by an indistinct constriction. The haptor bears four pairs of short pedunculated clamp-like suckers. The peduncles and suckers are of different sizes, the first pair being the smallest and the last pair the largest (figs. 27, 49). The most posterior peduncle is 75 μ long by 75 μ wide. The largest sucker is almost circular with a diameter of 45 to 50 μ, while the other suckers are elliptical in outline, 45 μ long by 25 μ wide. The characteristics of the cuticular structures could not be ascertained. Since the right half of the haptor, including the second, third and fourth suckers along with the posterior median part, has broken off, it is not possible to say whether the posterior end carries any hooks or not. Strong bands of muscles are seen in each peduncle of the sucker.

The oral aperture is subterminal. The pharynx is oval and muscular, 40 μ long by 34 μ wide, and is 28 μ below the median line drawn across the two oral suckers (fig. 44). The esophagus is very long. The intestine bifurcates at the middle of the body at about 1.3 mm from the anterior end of the body. Each caecum of the intestine branches and interbranches and seems to be entering the opisthaptor.

The genital aperture is about 200 μ from the anterior end of the body. The testes are not clearly seen but they appear to lie between a distance of 400 μ and 800 μ from the posterior end of the body. The anterior extremity of the testes is slightly above the posterior end of the ovary. The ovary is 600 μ long by 100 μ wide and lies on the right side of the median line. Near the genital aperture there is a conspicuously large ovoid body, probably an egg, 105 μ long by 75 μ wide. Vitelline follicles fill the spaces between the intestinal branches on either side.

DISCUSSION.

Linton (1905) reported *Dactylocotyle* sp. from the gills of *Brevoortia tyrranus* from North Carolina. He did not give a description but made an incomplete drawing showing only the posterior part of the body with an inscription 'X 66'. This drawing is reproduced herein (fig. 32). It shows four pairs of pedunculated suckers which are longer than those of the species described above, but this may be due to the power of contractibility of the peduncles. The length of the peduncles is not a permanent characteristic. Linton's drawing also shows the presence of a pair of lobes at the posterior end of the opisthaptor with a hook in each. It is not possible to say whether these lobes and hooks are present in the above described species since that part of the opisthaptor was broken off and lost during mounting. But from the shape of the haptor and the wide space between the series of suckers on each side it could be reasonably assumed that there was some structure at the posterior end of the opisthaptor. Hence the author assumes that Linton's *Dactylocotyle* sp. is a synonym of the species described above; this species is therefore named after him.

This is the first species of the genus to be reported from the Gulf of Mexico, and the third species from North America. The first two species reported from North America are *Diclidophora denticulata* (Olsson, 1876) Price, 1943, from the gills of *Pollachius virens* (Woods Hole and Nova Scotia), and *Diclidophora maccallumi* (Price, 1943) Sproston, 1946 from the gills of *Urophycis chuss,* taken from Woods Hole, Maine, and Canada.

World Distribution of the Genus. Atlantic coast of North America, Britain, Denmark, Belgian coast, Norway, and Mediterranean (i.e., Naples and Genoa).

Fam. DICLIDOPHORIDAE

Subfam. DICLIDOPHORINAE

13. *Diclidophora caudalis n.sp.*

Fig. 29

Host. Leiostomus xanthurus Lacépède—"Spot."
Location. Caudal fin.
Distribution. Port Aransas, Texas.
Number of specimens. One specimen secured from one host.
Holotype. U. S. N. M. Helm. Coll. No. 54760.

DESCRIPTION: The body is elliptical and is 1.95 mm long by 750 μ wide. The anterior haptor is not visible. The posterior haptor is distinct from the body, is 500 μ long by 550 μ wide, and bears four pairs of pedunculated suckers. The peduncles are of different lengths; the shortest is the anterior pair and the longest the posterior pair. The third and fourth on the left side appear to be the longest, 200 μ long by 100 μ wide. The diameter of the sucker varies from 100 μ to 140 μ. The peduncles of the first two pairs of suckers are extremely short. The exact nature of the cuticular supporting structures of the suckers cannot be made out, but they seem to be of the diclidophoran type.

The oral aperture is subterminal. The pharynx is 50 μ in diameter and is not very clear. The intestine has two caeca, each running along the margin of the body and giving off branches on either side. The two caeca seem to join at the posterior end in front of the haptor and the intestine enters the latter as a single canal, then divides into eight branches each one going to the peduncles of their respective sides.

Due to the opaque nature of the specimen the reproductive system could not be seen. Vitelline follicles do not enter the posterior haptor.

DISCUSSION.

The above description is by no means complete; the specimen being opaque, the reproductive system was not visible. But from the shape and structure of the opisthaptor this species is assigned to *Diclidophora*, and given the name *D. caudalis* because of its presence on the caudal fin of the host. In size this species closely approaches *Diclidophora macruri* (Brinkmann 1942) Sproston, 1946, reported from Skager-Rak and stated to be the smallest member of the genus, measuring 1.25 to 3.5 mm. long and 0.5 to 0.75 mm. in maximum width. But it differs from Brinkmann's species by the shorter peduncles, the difference in haptor measurements, and its presence on the caudal fin. This species is the first member of the genus to be reported from outside the branchial region and attacking the caudal fin of the host.

In assigning this species to the genus *Diclidophora* the writer has followed Sproston's (1946) practice in not recognizing the genus *Diclidophoroides* created by Price in 1943 and characterized by the presence of a distinct opisthaptor as opposed to *Diclidophora* having an indistinct opisthaptor.

This is the second species of the genus to be reported from the Gulf of Mexico and the fourth species from North America.

The world distribution of the genus is given under the description of *Diclidophora lintoni.*

Fam. HEXOSTOMATIDAE

14. *Hexostoma pricei n.sp.*

Fig. 9, 14, 38, 43, 46.

Host. Sarda sarda—"Common Bonito."
Location. Gills.
Distribution. Off Port Aransas, Texas.
Number of specimens. Four specimens secured from two of ten hosts examined.
Holotype. U. S. N. M. Helm. Coll. No. 54761.

DESCRIPTION: The body is elongate, 4.5 mm. long, 600 μ wide at the region 1.3 mm. from the anterior tip of the worm, 400 μ wide at the middle of the body, and 850 μ at the middle region of the opisthaptor.

The prohaptor consists of two elliptical suckers situated 25 μ from the anterior extremity of the body, each measuring 40 μ long by 30 μ wide, and opening into the oral cavity. The opisthaptor is not distinct from the body; it measures 750 μ at the anterior end and 850 μ at the middle broad region with the posterior end forming a semicircular outline. There are four pairs of oval suckers, the first two suckers 500 μ long by 340 μ wide, the third pair 460 μ by 340 μ, and the fourth pair 375 μ by 300 μ. Each sucker encloses three sclerites, the middle one X-shaped, while the two lateral ones are straight. The distance from the anterior end of the first sucker to the posterior end of the fourth sucker is 440 μ. Between the last pair of suckers there are two pairs of hooks, a small inner pair which is not very clear in the specimen (not shown in the drawing) and a comparatively long outer pair of branched hooks 145 μ long by 20 μ wide at the base, with a short branch at the middle, thus giving the appearance of the letter "C" mounted on an axis. The pointed ends of the hooks face away from the median line of the body.

The oral aperture is terminal. The pharynx is oval and non-muscular, 75 μ long by 45 μ wide. The intestine bifurcates at a distance of 500 μ from the anterior extremity of the body. Each caecum gives off branches on either side which again branch and interbranch forming a net-work. The two caeca are visible up to a short distance in front of the opisthaptor. Excretory apertures, which Price (1936) reports on the dorso-lateral side, are not visible in the specimens at hand.

The reproductive system is not visible on the specimens collected, only the vaginal opening being clear; this is dorsal and median in position, about 550 μ from the anterior end. Two distinct plates with their inner sides serrated, are seen in the vaginal opening; the right shorter plate is 55 μ long by 24 μ wide while the left longer plate is 70 μ long by 24 μ wide. The right plate at its anterior end is found to be about 10 μ ahead of the left plate.

DISCUSSION.

Linton (1901) described a worm *Hexacotyle thynni* De la Roche, 1811, from a single specimen collected on August 7, 1900, from the mouth of *Sarda sarda* by R. P. Cowles, but after examining one of the *H. thynni* (U.S.N.M. 9641) Price states in his Ph.D. thesis (1936, unpublished) that these two forms are distinct. After seeing the drawing of the author's Port Aransas specimen Price feels that it is a new species (personal communication). It probably is closely related to the specimen described by Linton but unfortunately in that specimen, according to Price, none of the internal organs could be made out. The variation in size of the suckers on the opisthaptor differentiates this Port Aransas species from all others. This specimen is named in honor of Dr. E. W. Price.

This is the second species of the genus Hexostoma to be reported from the Gulf of Mexico, the first, *Hexostoma macracanthum* being reported by Fujii in 1944 from the gills of *Euthynnus alletteratus* from Tortugas, Florida. Only one species of *Hexostoma* is so far reported from North America.

World Distribution. The genus *Hexostoma* contains nine species, two from the Mediterranean, one from the North Sea, one from Galapagos Islands, two from North America (including the present species) and three from Japan.

SUMMARY

A survey is made of the monogenetic trematodes of three hundred twenty-seven fish, belonging to forty different species, from Port Aransas.

Fourteen species, consisting of eight new species and four old species, belonging to seven different families, are recorded and described. At the end of each description a short discussion is made of the distribution of that species and genus in the Gulf region, in North America and in the world in general. The following are the Monogenea described with their respective hosts.

1. *Dionchus hopkinsi n.sp.* ex *Rachycentron canadus,* 2. *Encotyllabe pricei n.sp.* ex *Scorpaena plumieri,* 3. *Microcotyle scomberomori n.sp.* ex *Scomberomorus maculatus,* 4. *Pseudaxine texana n.sp.* ex *Scomberomorus maculatus,* 5. *Heteraxine scomberomori n.sp.* ex *Scomberomorus maculatus,* 6. *Diclidophora lintoni n.sp.,* ex *Brevoortia gunteri,* 7. *Diclidophora caudalis n.sp.* ex *Leiostomus xanthurus,* 8. *Hexostoma pricei n.sp.* ex *Sarda sarda.* 9. *Loimos scoliodoni* Manter, 1944 ex *Scoliodon terrae-novae* and *Carcharhinus limbatus,* 10. *Squalonchocotyle tiburonis* Brooks, 1934, ex *Sphyrna tiburo,* 11. *Protomicrocotyle mirabilis* Johnston and Tiegs, 1922, ex *Caranx hippos,* 12. *Metamicrocotyla macracantha* (Alexander, 1954) n.comb. ex *Mugil cephalus,* 13. *Pyragraphorus incomparabilis* (MacCallum, 1917) n.comb., ex *Caranx hippos,* 14. *Microcotyle pomatomi* Goto, 1899 ex *Pomatomus saltatrix.*

REFERENCES

Alexander, C. G.
1954. *Microcotyle macracantha* n.sp., a monogenetic trematode from the Gulf of California, with a redescription of *Amphibdelloides maccallumi* (Johnston and Tiegs, 1922) Price 1937. J. Parasit. 40 (3) : 279–283.

Abdel Azim, M.
1939. Note sur *Microcotyle cephalus* n.sp. ectoparasite des arcs branchiaux de *Mugil cephalus.* Ann. Parasit. 17: 17–20.

Breder, C. M., Jr.
1948. Fieldbook of Marine Fishes of the Atlantic Coast. G. P. Putnam's Sons, New York.

Brinkmann, A., Jr.
1942. On some new and little-known *Dactylocotyle* species, with a discussion on the relations between the genus *Datcylocotyle* and the "family" Diclidophoridae. Göteborgs Mus. Zool. Avdelning 92: Göteborgs Vitensk. samh. Handl. Sjätte Följden, ser. B, 1: 1–32.

Brooks, G. L.
1934. Some new ectoparasitic trematodes (Onchocotylinae) from the gills of American sharks. Parasitology 26: 259–67.

Chauhan, B. S.
1945. Trematodes from Indian marine fishes. Part I. On some new monogenetic trematodes of the suborders Monopisthocotylea Odhner, 1912 and Polyopisthocotylea Odhner, 1912. Proc. Indian Acad. Sci., Sect. B, 21: 129–159.

Chauhan, B. S. & Bhalerao, G. D.
1945. *Loimos secundus* (Monogenea, Trematoda) from the gills of the common Indian dogfish *(Scoliodon sorrakowah).* Proc. Indian Acad. Sci., Sect. B, 22: 164–167.

Dawes, B.
1946. The Trematoda. Cambridge University Press, London, 644 pp.

Fujuii, H.
1944. Three monogenetic trematodes from marine fishes. Jour. Parasit. 30: 153–158.

Goto, S.
1896. On some ectoparasitic trematodes from the Atlantic coasts of the United States of North America. Compt. Rend. 3me. Congr. Internat. Zool., Leyden (1895) : 351–352.

Johnston, T. H. & Tiegs, O. W.
1922. New gyrodactyloid trematodes from Australian fishes, together with a reclassification of the superfamily Gyrodactyloidea. Proc. Linn. Soc. N. South Wales 47: 83–131.

Linton, E.
1905. Parasites of fishes of Beaufort, North Carolina. Bull. U.S. Bur. Fish. 24, 321–428.

———.
1940. Trematodes from fishes mainly from the Woods Hole region, Massachusetts. Proc. U.S. Nat. Mus. 88: 1–172.

MacCallum, G. A.
1913. Notes on four trematode parasites of marine fishes. Centralbl. Bakteriol., 1 Abt. Orig. 70: 407–416.

———.
1915. Some new species of ectoparasitic trematodes. Zoologica, N.Y. 1: 393–410.

———.
1916. Some new species of parasitic trematodes of marine fishes. Zoopathologica 1: 3–38.

———. 1917. Some new forms of parasitic worms. Zoopathologica 1: 43–75.

———. 1918a. Notes on the genus *Telorchis* and other trematodes. Zoopathologica 1: 77–98.

———. 1918b. Studies on the Polystomidae. Zoopathologica 1: 103–120.

———. 1921. Studies in Helminthology. Part I. Trematodes. Zoopathologica 1: 135–204.

Manter, H. W.
1938. Two new monogenetic trematodes from Beaufort, North Carolina. Livro Jub. Prof. Travassos, Brazil, 3: 293–298.

———. 1944. Notes on the trematode subfamily Loimoinae (Monogenea) with a description of a new genus. Jour. Wash. Acad. Sci. 34: 86–89.

Manter, H. W., & Prince, D. F.
1953. Some monogenetic trematodes of marine fishes from Fiji. Proc. Helminth. Soc. Wash. 20: 105–112.

Meserve, F. G.
1938. Some monogenetic trematodes from the Galapagos Islands and the neighboring Pacific. Allan Hancock Pacif. Exped. (Univ. S. Calif. Publ.) 2: 29–88.

Price, E. W.
1936. North American monogenetic trematodes. Geo. Wash. Univ. Bull. (Summaries of Doctoral Theses, 1934–36): 10–13.

———. 1942. North American monogenetic trematodes. V. The family Hexabothriidae, n.n. (Polystomatoidea). Proc. Helminth. Soc. Wash. 9: 39–56.

———. 1943. North American monogenetic trematodes. VI. The family Diclidophoridae (Diclidophoroidea). J. Wash. Acad. Sci. 33: 44–54.

Remley, L. W.
1936. Morphology and life-history studies of *Microcotyle spinicirrus*, a monogenetic trematode on the gills of *Aplodinotus grunniens*. Jour. Parasit. 22 (Suppl.) 535–536. (Abstr.)

———. 1942. Morphology and life-history studies of *Microcotyle spinicirrus* MacCallum, 1918, a monogenetic trematode parasitic on the gills of *Aplodinotus grunniens*. Trans. Amer. Micr. Soc. 61: 141–155.

Sproston, N. G.
1946. A synopsis of the monogenetic trematodes. Trans. Zool. Soc. London 25 (4): 185–600.

Yamaguti, S.
1953. Parasitic worms mainly from Celebes. Part 2. Monogenetic trematodes of fishes. Acta Medicinae Okayama 8 (3): 203–256.

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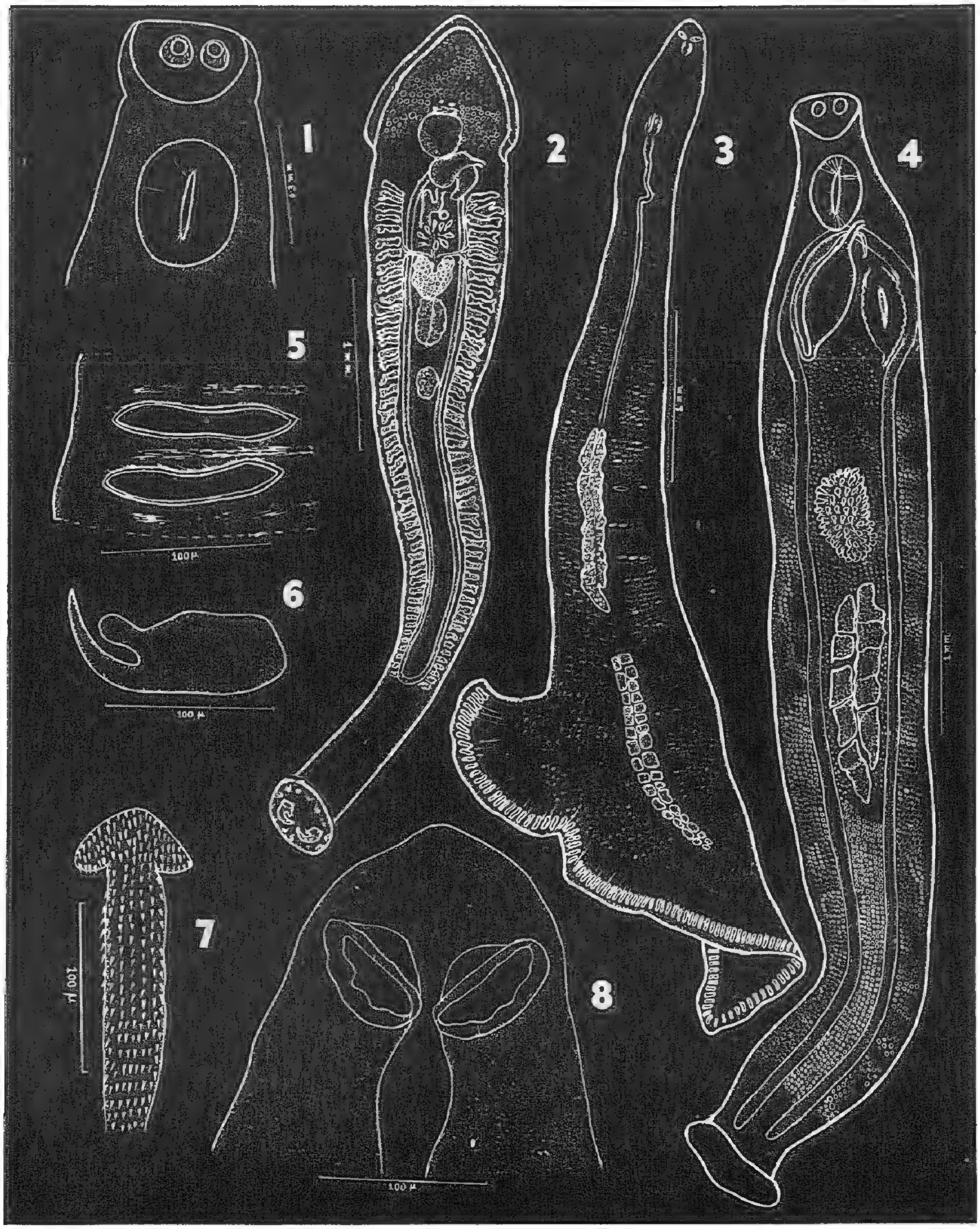
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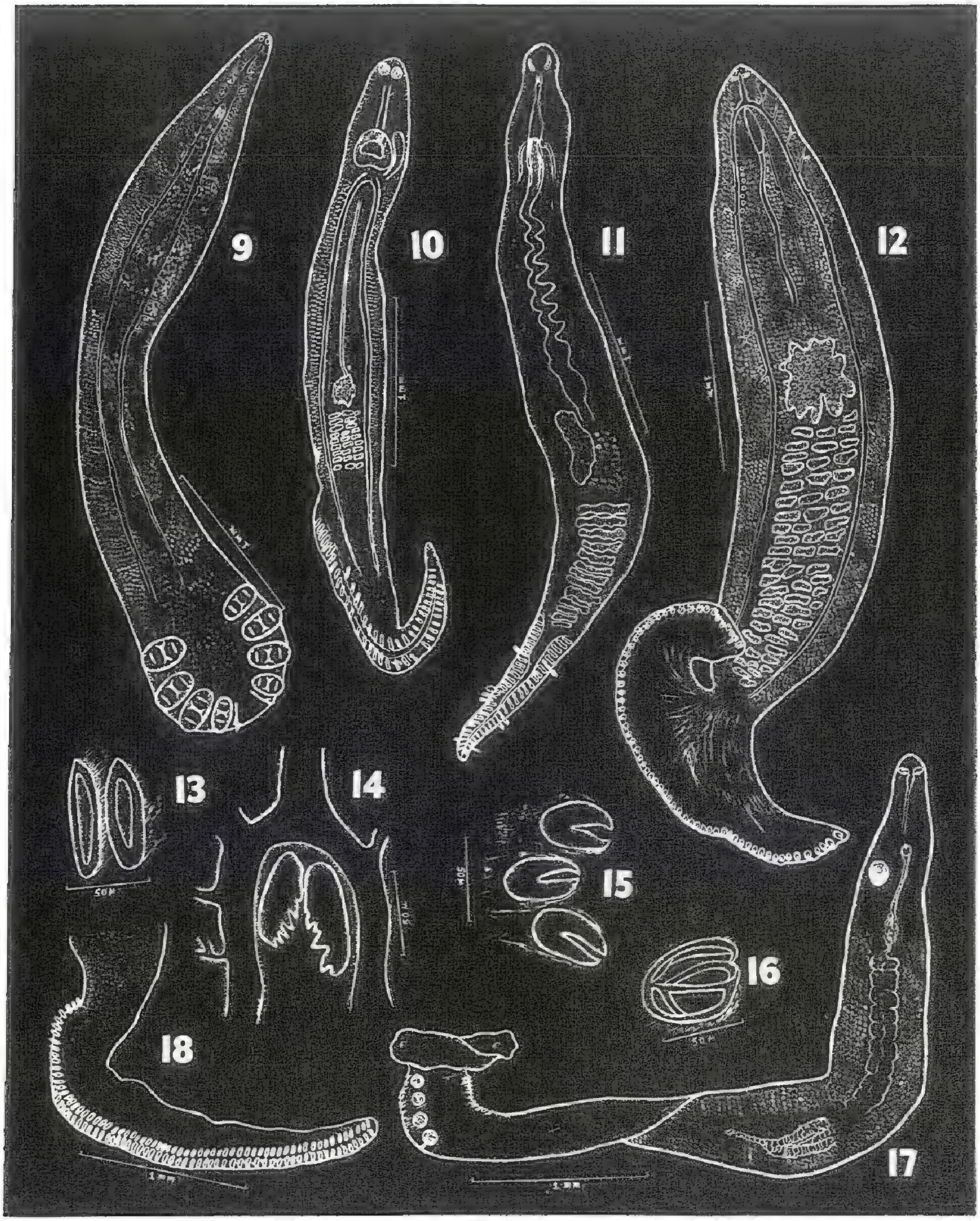
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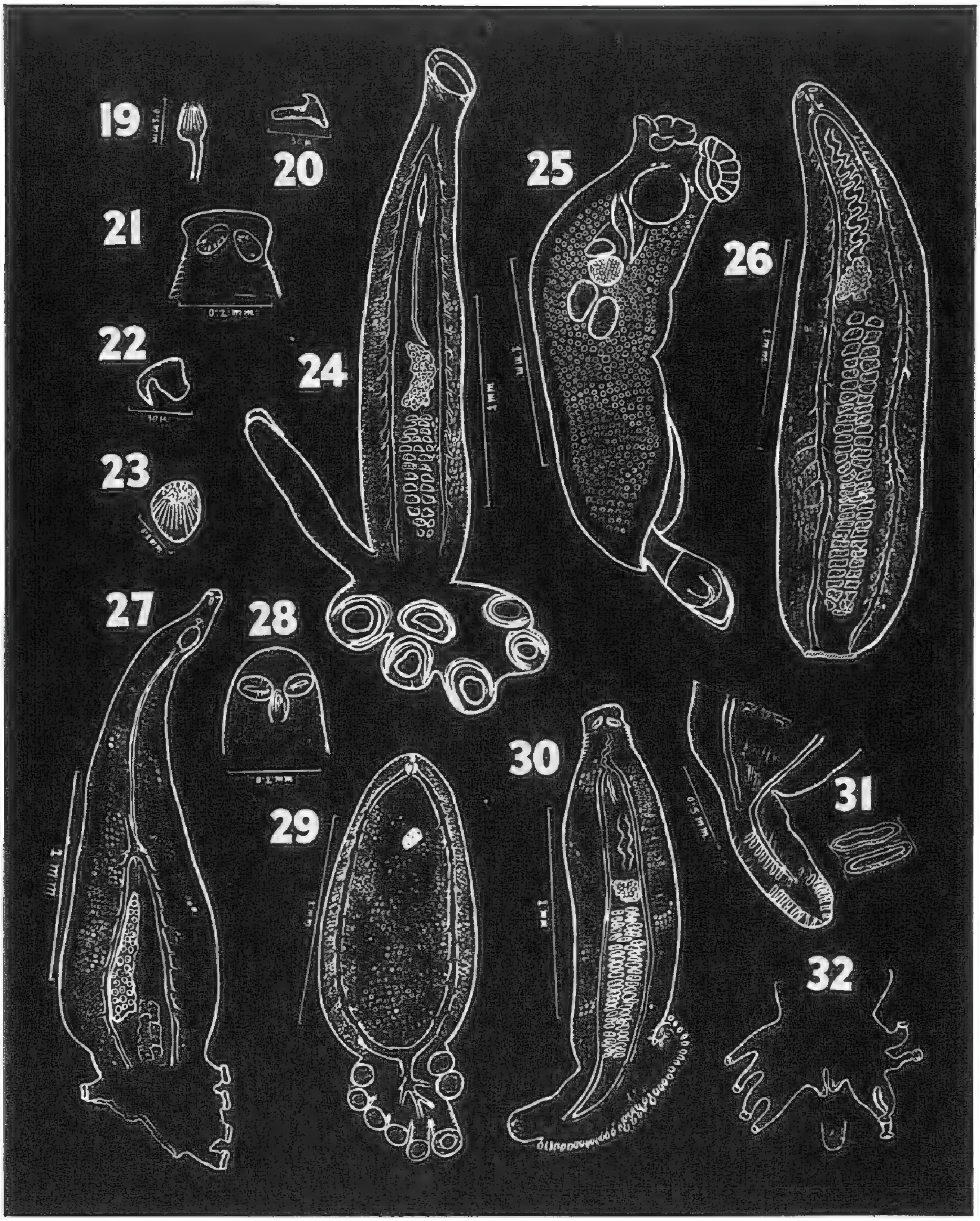
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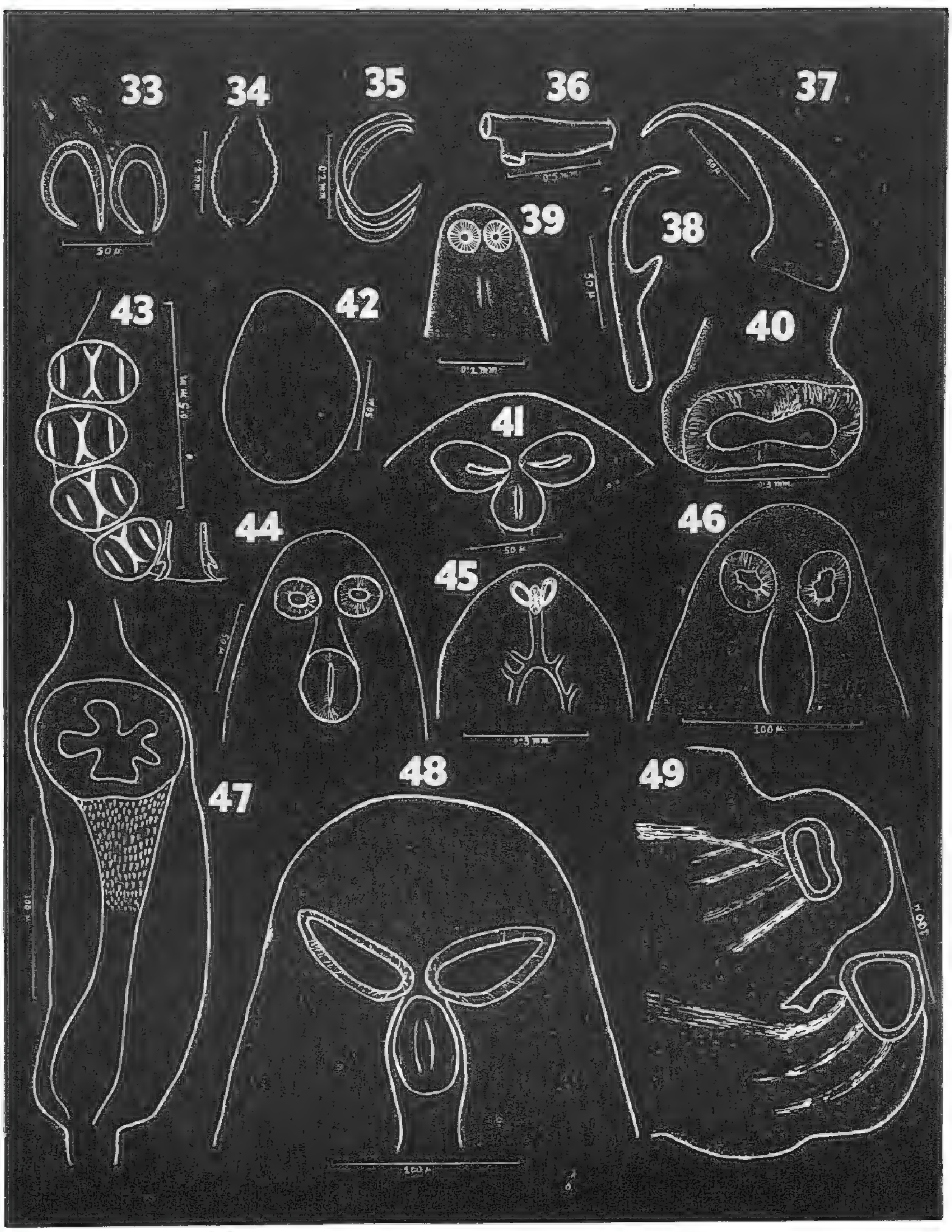
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A Study of the Oyster Biology and Hydrography At Crystal River, Florida

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INTRODUCTION

From 1949 through 1954 a number of investigations were conducted in Florida on the biology of the oyster, *Crassostrea virginica* (Gmelin), and on the hydrography of the producing or previously productive areas. The results of studies in Tampa Bay and Cedar Keys, both sub-marginal in oyster production, and in Apalachicola Bay, the acknowledged center of Florida's oyster industry, have been published in a number of papers by the present author and R. M. Ingle. While each of these regions differ in mean depth, area, and quality and quantity of production, all may be considered as regions of high salinity for this species of oyster.

Early in 1951 it was decided that similar investigations should be extended to a low salinity area, with the hope that the results could be applied to the future State or private oyster culture programs.

The choice of a study area was limited to the west coast of Florida. Although certain east coast localities satisfy the salinity requirement and some occasionally report a significant oyster production, the future of Florida's east coast oyster industry is not promising. The rapid industrialization and urbanization of the east coast and the concomitant increase in industrial and sewage pollution has resulted in the closure of many formerly productive grounds. The relatively high economic level of this area has also led to lack of interest in the production of east coast oysters. Florida law restricts the oyster fishery to the use of hand tongs or to wading ("hogging," in the Florida vernacular) oysters in shallow water and these methods are among the hardest types of manual labor. As a result of the unstable demand and availability of the east coast oyster, the former oysterman, or present-day potential oysterman has found that he is assured a much higher monetary return at greatly reduced effort by working as a common laborer or by peddling trinkets to tourists.

With the study area limited to the west coast, the choice naturally fell to Crystal River and the adjacent waters. This locality fulfilled the salinity requirement, supported a comparatively good oyster production, and had the further advantage of being relatively isolated. This augurs well for at least the temporary continuation of the natural environment with little change by human agencies.

The Crystal River region has long been noted for the production of high quality oysters, but it has not been subject to more than casual interest by oyster biologists. Aside from various statistical reports, published references to the area are scarce. Ruge (1898), however, recognized potentialities for oyster production in the region by his statement, ". . . and Crystal River, in which vicinity the physical features are preeminently favorable for oyster cultivation." It is reported that the beds supported an oyster cannery during the early part of the century, and a public stock company, Crystal River Oyster Farms, was established during the late thirties or early forties. Although commercial grade oysters were produced, using closely spaced wooden stakes for setting surfaces, financial difficulties and the predation of oyster pirates forced the termination of this venture within five years. Since 1945 Citrus County (Crystal River) has been among the top five oyster producing counties of Florida, and for at least three years ranked second to Apalachicola. The average reported annual production for the years 1950 through 1954 was roughly 44,000 pounds of meats.

From the end of August 1951 until the latter part of August 1952, the author worked continuously in the estuary of Crystal River. This paper presents the results of studies on the salinity and temperature characteristics and oyster biology of the region during this period. The work was supported by the Florida State Board of Conservation as a part of its oyster rehabilitation program.

The author wishes to express his appreciation for the assistance rendered by Mr. James Daniels and the other cooperative citizens of Crystal River. Credit is due Mr. W. S. Shoemaker for the photograph in Plate 1 and special thanks are due Mary Rose Dawson for her active assistance throughout the study period.

METHODS

Twenty sampling stations were established in the survey area (Figure 1). These were located with the view of achieving representative coverage of both the inshore and offshore waters by stations amenable to frequent sampling by a single observer. Station names are derived from nearby charted objects such as the various Coast and Geodetic Survey daymarkers in the Crystal River channel, or in reference to charted and easily identifiable landmarks or natural features.

TABLE 1

Monthly distribution of salinity samples and surface temperature observations, September 1951 through August 1952.

		SALINITY			TEMPERATURE	
Month	Stations occupied	Sampling Days	Surface Obs.	Bottom Obs.	Total Obs.	Surface Obs.
Sept., 1951	19	6	31	1	32	37
Oct.	13	14	111	6	117	118
Nov.	20	17	193	8	201	193
Dec.	20	14	182	6	188	182
Jan., 1952	20	16	205	10	215	205
Feb.	20	8	108	3	111	110
Mar.	20	9	124	12	136	124
Apr.	20	9	107	6	113	107
May	20	12	153	16	169	153
June	20	10	132	13	145	132
July	20	12	127	6	133	127
Aug.	20	5	40	0	40	40
Total	20	132	1,513	87	1,600	1,528

All salinity and temperature observations were made from an outboard motorboat, and up to fifteen stations were visited per sampling day. Observations were made on 132 days during the period, with sampling days ranging from five to seventeen per month. An analysis of the sampling distribution is shown in Table 1. Density and temperature observations were made *in situ* with hydrometers and thermometers. Conversion to salinity was made from these readings. Bottom water samples were obtained with a Foerst water sampler.

Oysters for growth rate studies were held in baskets made of one-inch galvanized hardware cloth approximately sixteen inches wide, twenty-two inches long and four inches deep. The baskets were furnished with hardware cloth covers which were securely fastened after each inspection. The baskets were carried approximately four inches off the bottom in individual wooden frames rigidly suspended from a supporting structure of six inch piling and two by six planks. Six of these baskets were set out at each of the two growth rate stations. Only one basket was removed from the water at a time. The maximum length of each oyster was measured to the nearest millimeter by calipers; the oyster was returned to the basket and the data recorded. The basket was replaced, if evidences of corrosion warranted, the cover was then secured and the basket was returned to the water. Every effort was made to reduce exposure time to a minimum, and precautions were taken to avoid rough handling of either the loaded baskets or the individual oysters. All measurements were obtained with the same calipers, and thereby one source of error suggested by Lunz (1951) was eliminated. The oysters used were obtained in the immediate vicinity of the station.

Spat collectors were made of chicken wire baskets filled with bleached shell. These were exposed for an average period of fifteen days and then returned to the laboratory for examination under a low power microscope. Spat counts were made from the inner surfaces of twenty shells selected at random from each collector.

OBSERVATIONS

a) *Description of Area*

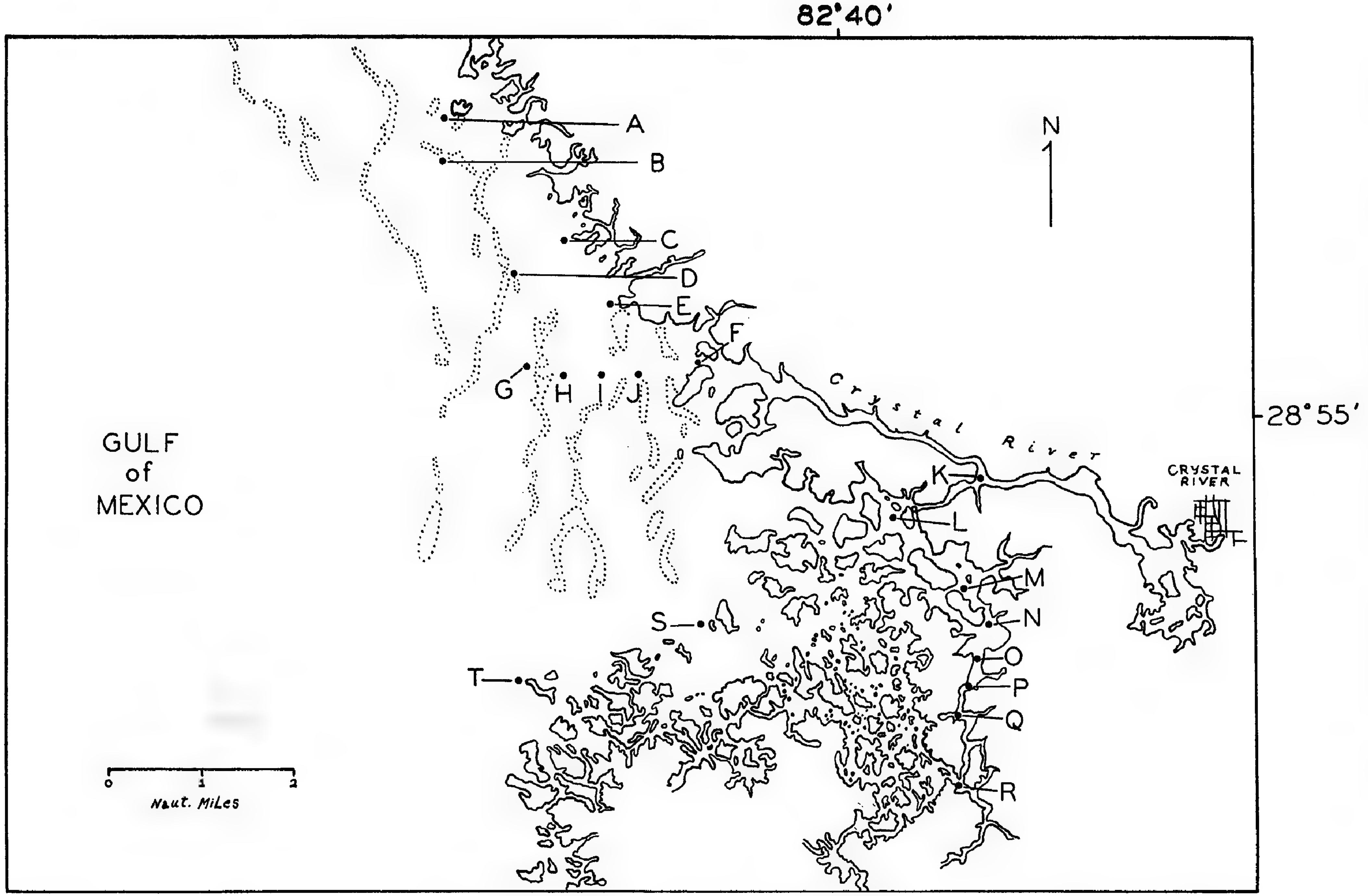
The town of Crystal River is located at the headwaters of the Crystal River in Citrus County on the Florida west coast, approximately ninety highway miles north of St. Petersburg.

The Crystal River is a spring-fed stream, some six miles long, which discharges partly into a slight indentation of the Gulf coast known as Crystal Bay, and partly through a branch waterway, Salt River, into an assemblage of islets and marshes to the south and west of Crystal River (Figure 1). There is a narrow channel dredged to a controlling depth of six feet, at the mouth of the river and through the offshore oyster bars, which permits the passage of small boats. There is direct connection through the Salt River with the Homosassa River some eight miles to the south. The Withlacoochee River flows into the Gulf about six miles north of the Crystal River, but there is no direct connection between the two.

As indicated by the station locations, the area covered by the present study includes the waters of Crystal Bay from Mangrove Point on the south to Drum Island on the north, and the marsh or "backswamp" territory south of the Crystal River to the station designated as South Narrows.

The entire region is within the drowned karst subsector of the Gulf coast as defined by Price (1954a). Characteristically there is a general absence of sand beaches. The bottoms of Crystal Bay consist of various mixtures of sand, mud and broken oyster shell; whereas those of the Salt River or backswamp region are predominately of deep, soft mud. The numerous rocky and marshy islets, located south of the Crystal River, support a varied and dense vegetation ranging from marsh grass to live oak, cedar, cabbage palm, palmetto and the prickly pear cactus. Davis (1940) reported the presence of both red and black mangroves in Crystal Bay, and during this study mangroves were found as far inshore as Dixie Bay in the Salt River.

As the name implies, the waters of the Crystal River are exceedingly clear and under good conditions it is possible to see bottom distinctly in depths exceeding fifteen feet. Although water transparency in Crystal Bay is largely influenced by weather conditions,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CRYSTAL RIVER
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Figure 1. Chart of the Crystal River area showing survey stations and general location of offshore reefs. Letter key for stations as follows: *A*—Drum Island; *B*—Demory Gap; *C*—Negro Island; *D*—Tin Pan Gap; *E*—Black Point; *F*—Shell Island; *G*—Mkr. #5; *H*—Mkr. # 10; *I*—Mkr. # 12; *J*—Mkr. #16; *K*—Salt River Branch; *L*—Big Coon Gap; *M*—Lewis Creek; *N*—N. Dixie Bay; *O*—S. Dixie Bay; *P*—N. Narrows; *Q*—Mid Narrows; *R*—S. Narrows; *S*—Mullet Key; *T*—Mangrove Point.

visibility frequently exceeds five feet. An entirely different situation prevails in the backswamp region; here it is consistently impossible to see bottom in depths greater than eight inches and the waters are commonly of a muddy hue indicating a high sediment load.

The waters are exceptionally shoal throughout the territory. Aside from a single "hole" in excess of fifteen feet at the north end of Dixie Bay, depths throughout the backswamp average less than two feet at MLW. Soundings of seven or eight feet are found in the offshore inter-bar waters of Crystal Bay and relatively deep water may be found in the gaps or cuts through the oyster bars, but the average depth for the study area does not exceed three feet. In addition to the normally shoal character of the backswamp, those bottoms support numerous oyster bars ranging in height from six inches to three feet above the surrounding bottom. Such bars vary in size from scattered clumps to shell and coon oyster beds several hundred feet long. The water is so shallow in the backswamp territory that it is next to impossible to navigate the region, even with a small outboard, without considerable local knowledge.

Situated in a roughly north-south direction across Crystal Bay and extending up to three and a half miles into the open Gulf of Mexico off the mouth of the Crystal River is a series of approximately five long oyster reefs, the Crystal Reefs. These are not continuous bars, but are broken by numerous gaps or cuts. Much of this reef complex is continuously exposed except during periods of spring high tides, and the tops of the individual segments usually consist of dead shell (Plate 1). Oysters varying in quality from commercial grades to the ubiquitous coon clumps grow along both the inshore and offshore edges of these reefs. The oyster population is, in fact, largely limited to the reef flanks and the bottoms immediately surrounding the bars, and the inter-bar bottoms are usually devoid of oyster growth. These observations are in agreement with those made by Price (1954b) on other offshore reefs in the open Gulf. This reef complex roughly parallels the coast and extends from just north of Mangrove Point to Porpoise Point in Withlacoochee Bay, a distance of approximately thirteen miles.

b) *Climate, Tides and Springs*

Unfortunately, there are no available weather records for Crystal River and even those of the reference station are incomplete for the study period. The nearest weather station supplying temperature and precipitation data is located at Inverness, approximately eighteen miles west of Crystal River. Precipitation data for Inglis, at the mouth of the Withlacoochee River, is available for the years 1942 through 1947. In view of its proximity to the coast, it may be assumed that the climate of Crystal River is less extreme than that of Inverness, but for present purposes all references to air temperatures will be to those of the Inverness record.

The mean annual air temperature over the twenty year record is 71.3° F., and the maximum and minimum records are 103.0° F. and 17.0° F., respectively. Maximum temperatures are experienced during July and August and minimums during December and January.

The mean annual precipitation at Inverness is 56.03 inches and that for the 1942-47 period at Inglis is 45.67 inches. Better than sixty per cent of the annual precipitation occurs during the months of June through September, and most of this is in the form

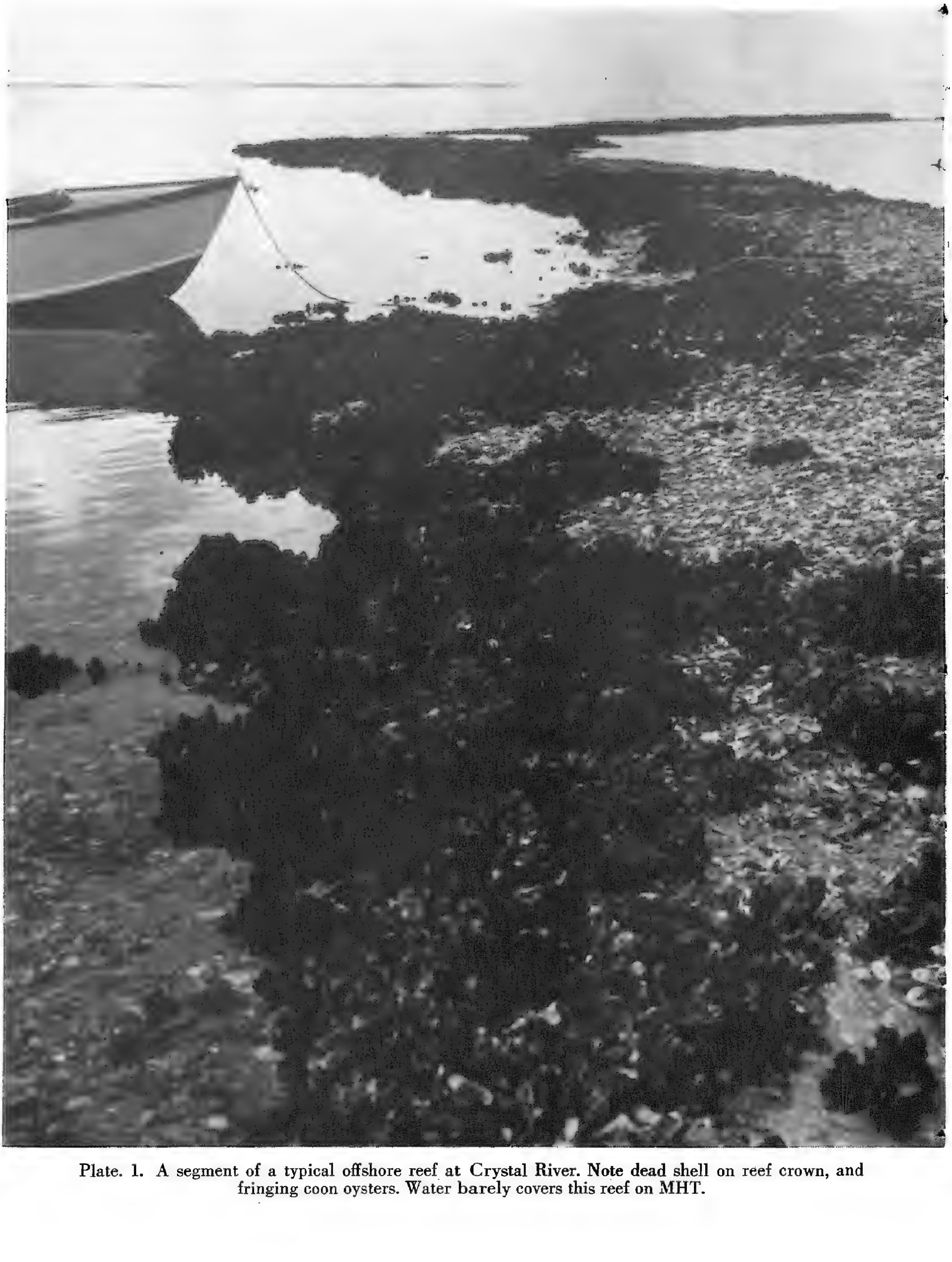

Plate. 1. A segment of a typical offshore reef at Crystal River. Note dead shell on reef crown, and fringing coon oysters. Water barely covers this reef on MHT.

of heavy afternoon thunderstorms. Visher (1954) shows that Crystal River lies within the zone of maximum thunderstorm frequency and from eighty to ninety storm days per year can be expected there.

The mean monthly air temperatures during the study period and for the twenty year record are shown in Figure 2, together with the total monthly precipitation for Inverness and Inglis.

During winter months, night and morning fog is frequent over the river and the backswamp, but this is usually dissipated by early afternoon. Moderate temperature drops accompany winter northers, but low temperatures seldom persist for more than two or three days at a time. There is no available data on wind conditions in the area. Winds at Tampa, some eighty miles to the south, are predominately northeasterly in winter and easterly during the summer months and have a mean annual velocity of approximately 8.4 miles per hour (U. S. Coast Pilot). Tropical hurricanes occasionally strike the area and at such times the accompanying heavy rains and high tides may flood the entire coastal region as far east as the town of Crystal River.

TABLE 2

Summary of surface salinity observations; term and weekly; September 1951 through August 1952.

Station	Total Obs.	Maximum Salinity in o/oo	Minimum Salinity in o/oo	Mean Salinity in o/oo	σ	Weekly Obs.	Maximum Weekly Range in o/oo	Mean Weekly Range in o/oo
Salt River Branch	196	12.0	0.0	2.2	1.8	106	12.0– 1.4	1.8
Shell Island	84	17.0	1.2	7.1	4.1	40	16.1– 3.4	4.0
Marker #16	58	22.3	3.2	12.1	4.0	28	22.3–10.5	4.1
Marker #12	61	23.1	4.1	13.8	2.7	29	17.0– 5.1	4.4
Marker #10	59	22.5	6.8	15.6	4.1	30	20.2– 7.7	3.5
Marker #5	64	28.4	9.8	18.1	4.0	30	21.9–11.0	3.8
Big Coon Gap	143	20.9	4.3	10.2	2.5	84	20.9–11.4	2.4
Lewis Creek	98	15.4	7.3	11.0	1.5	58	14.0– 7.9	1.8
N. Dixie Bay	96	15.7	8.0	11.4	1.3	54	14.3– 8.0	1.4
S. Dixie Bay	97	15.5	7.7	12.2	1.3	48	14.3– 7.7	1.2
N. Narrows	122	15.9	7.0	13.0	1.2	48	14.2– 7.0	1.2
Mid Narrows	93	17.5	6.8	12.7	2.0	43	14.5– 6.8	1.4
S. Narrows	103	19.6	5.8	14.2	2.1	39	16.3– 5.8	1.5
Black Point	55	19.0	6.3	12.8	2.8	10	16.4–11.3	2.4
Negro Island	25	20.5	8.0	14.8	3.6	4	18.8–15.2	1.8
Demory Gap	31	26.6	10.9	17.1	4.9	2	23.8–21.3	2.2
Drum Island	34	25.1	9.5	17.4	4.6	3	23.0–18.6	3.3
Tin Pan Gap	37	27.8	12.4	18.0	3.4	8	19.9–16.6	1.9
Mullet Key	30	23.4	13.0	16.6	3.6	3	19.3–17.1	1.5
Mangrove Point	27	26.9	13.5	18.5	3.6	3	18.3–13.5	2.4

Crystal River is not listed in the Tide Tables, but the "Coast Pilot" reports the mean tide range at the river mouth to be about two and a half feet. Personal observations support this statement. It was observed that northers with velocities estimated at less than thirty miles per hour generated perceptible wind tides of some magnitude. This was particularly noticeable in the Salt River where low tides made the area all but impassable. It should be further noted that moderate westerly and southwesterly winds result in higher than normal tides throughout the region. The effects of both astronomical and meteorological tides are apparent as far upstream as the headwaters of the Crystal River. Tidal currents are relatively swift and at such restricted localities as in the gaps, at the river mouth and in the Salt River they may attain velocities estimated in excess of four knots.

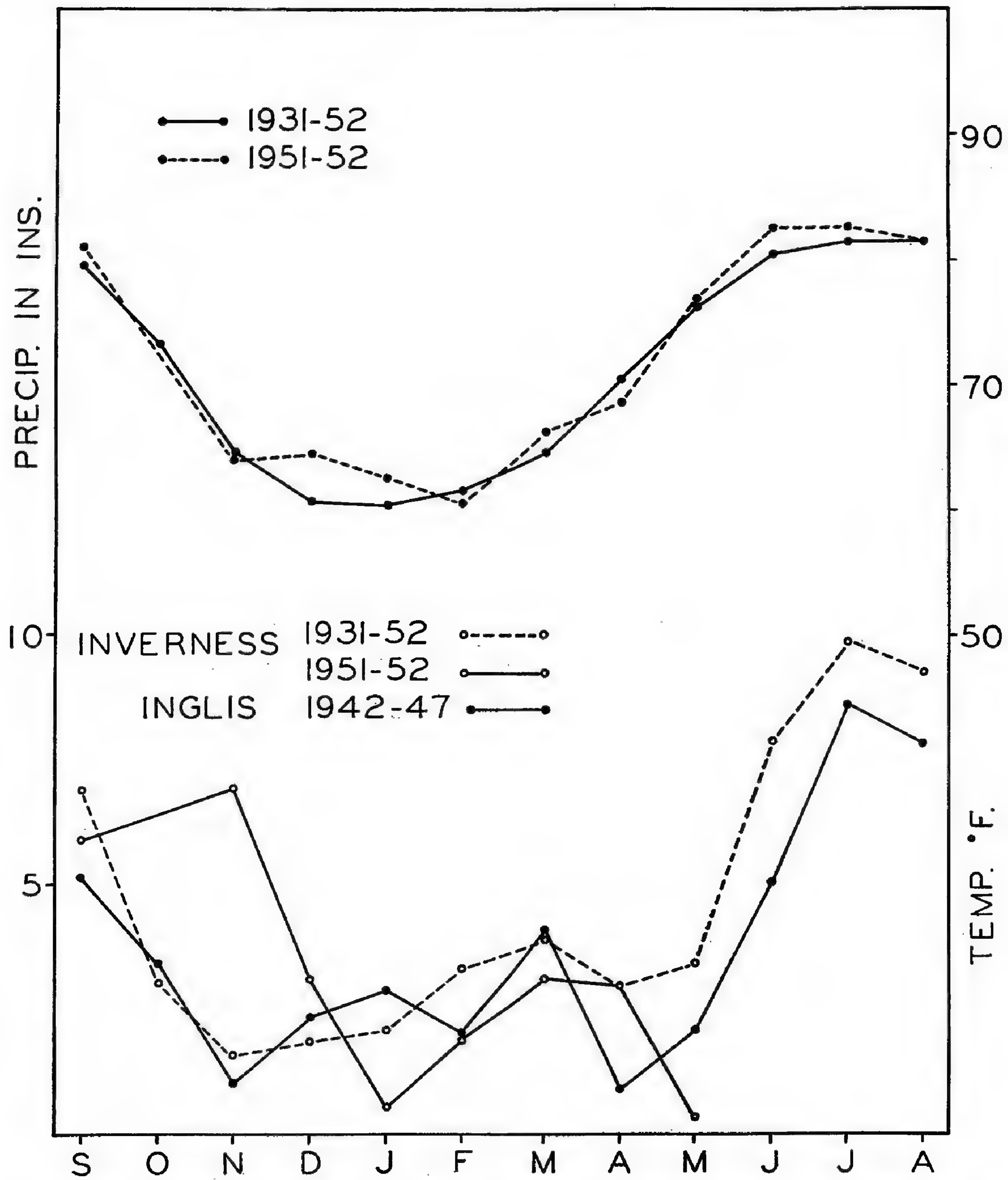

Figure 2. Monthly precipitation and air temperature data at Inverness during survey period and over 20 year record. Precipitation at Inglis for 1942–47.

The Crystal River is primarily spring-fed, but no references have been located describing the springs in detail. Ferguson *et al.* (1947) describe but one, Hunter Spring, at Crystal River and report a flow of 41 million gallons per day. Vernon (1951) reports that the river is almost entirely spring-fed and that the area under consideration is within a discharge area of the Florida artesian ground-water system. According to the Florida Geological Survey no further data is available. Personal observation has shown that springs occur not only at the head of the Crystal River, but at least as far downstream as the Salt River Branch station.

TABLE 3

Summary of serial salinity and temperature observations. Temperatures refer to surface samples only. Depth at Tin Pan Gap is approximately six feet at MLW.

Station	Date	Hourly Samples	Salinity Range in o/oo	Mean Salinity in o/oo	Temp. Range in ° C.	Mean Surface Temp. in ° C.
N. Narrows	11–7/ 8–51	25	13.5–15.7	14.3	11.0–19.5	15.8
S. Narrows	12–5/ 6–51	25	12.9–14.7	13.8	20.0–24.0	21.4
Black Point	1–15/16–52	25	11.1–17.0	13.4	15.5–20.5	16.8
Tin Pan Gap (Surface)	5–26–52	10	15.1–19.6	17.3	20.8–29.5	28.9
Tin Pan Gap (Bottom)	5–26–52	10	15.7–19.9	18.0	28.0–30.0	29.0

Although no flow data is available, the continuous surface slicks and roils at numerous locations in the river indicate that the total flow must be of a high order and is probably even greater than the mean recorded flow of 120 million gallons per day at Homosassa Springs (Ferguson *et al.*, 1947). While no specific search was made during this study, springs were not observed in either the backswamp or in Crystal Bay.

TABLE 4

Summary of concurrent surface and bottom salinity observations. The term "difference" refers to the bottom salinity minus the surface salinity. Depth at each station was approximately six feet at MLW.

Station	No. Obs.	Mean Surface Salinity in o/oo	Mean Bottom Salinity in o/oo	Maximum Difference in o/oo	Mean Difference in o/oo
Shell Island	10	6.2	7.0	4.2	0.8
Marker #16	10	11.4	13.5	6.8	2.1
Marker #12	10	13.2	14.9	4.0	1.7
Marker #10	10	15.1	16.4	4.5	1.4
Marker #5	11	18.6	19.1	2.0	0.5
Tin Pan Gap	13	17.3	17.6	3.1	0.5

c) *Salinity and Temperature*

A total of sixteen hundred surface and bottom salinity observations were made at twenty stations during the period from September, 1951, through August, 1952. Due to a scarcity of stations with sufficient depth to warrant bottom sampling, such observations totaled but eighty-seven for the entire study. A summary of all surface salinity observations, together with data on weekly salinity variation is shown in Table 2. The term "weekly range" as used here refers to variation observed during any seven day period. In Figure 3 the surface salinity mean and range for each station is shown as a haligraph, modified after Stauber (1943).

Serial salinity and temperature observations were made at four stations. Hourly samples were taken in each case, and at three stations the sampling was continued through the entire tidal cycle. The data thus obtained is summarized in Table 3. In addition to samples obtained at the Salt River Branch station, to be discussed below, concurrent surface and bottom salinity data were collected at six stations and are summarized in Table 4.

The monthly maximum, minimum and mean surface temperatures, together with the available monthly mean air temperatures at Inverness are shown in Table 5. No bottom

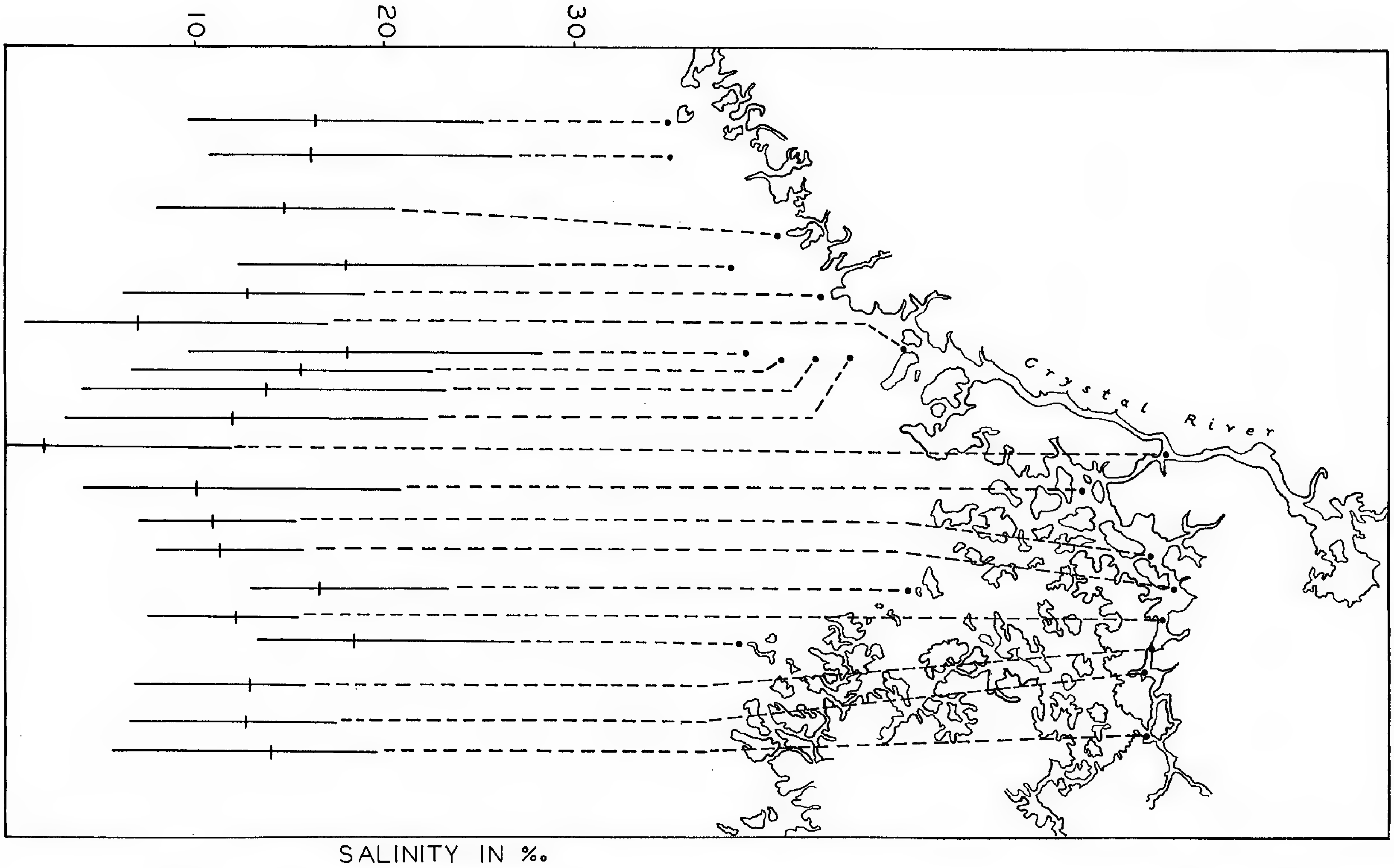

Figure 3. Haligraph showing surface salinity means and ranges at all stations, September 1951 through August 1952. Perpendicular solid line shows salinity range and cross-bar indicates the mean. Stations are, from left to right, Drum Island, Demory Gap, Negro Island, Tin Pan Gap, Black Point, Shell Island, Marker #5, Marker #10, Marker #12, Marker #16,, Salt River Branch, Big Coon Gap, Lewis Creek, N. Dixie Bay, Mullet Key, S. Dixie Bay, Mangrove Point, N. Narrows, Mid Narrows and S. Narrows.

temperature observations of sufficient accuracy for surface-bottom comparisons were obtained.

d) *Growth Rate and Mortality of Oysters*

Growth studies were made at three stations: Dixie Bay, South Narrows and Tin Pan Gap. Since the Tin Pan Gap growth station was completed late in the period and insufficient measurements were made, the data for this station is not presented here. The Dixie Bay and South Narrows studies were, respectively, initiated in November and December, 1951. Aside from Basket #5 at the South Narrows station, which was last measured in June, all measurements were made at approximately thirty-one day intervals until July, 1952.

TABLE 5

Monthly maximum, minimum and mean surface water temperatures over study area, and recorded mean air temperatures at Inverness, September 1951 through August 1952.

Month	Total Obs.	Maximum Temp. °C.	Minimum Temp. °C.	Mean Temp. °C.	Mean Inverness Air Temp. °C.
Sept., 1951	37	30.5	24.5	29.3	27.2
Oct.	118	28.5	24.8	25.2	....
Nov.	193	25.5	11.0	17.7	17.9
Dec.	182	24.0	13.0	19.0	18.0
Jan., 1952	205	24.0	13.0	17.4	16.9
Feb.	110	21.5	15.0	18.1	15.9
Mar.	124	23.0	13.0	20.8	19.0
Apr.	107	25.5	18.0	21.9	20.3
May	153	30.5	22.5	26.7	24.9
June	132	32.0	27.0	29.9	28.3
July	127	33.0	28.0	30.0	28.3
Aug.	40	32.0	26.0	29.8	27.7

Especial care was taken at the establishment of each growth station to select oysters exhibiting normal growth characteristics; no scissor-bills or coon oyster were included. As will be noted in Table 6, the initial sizes were selected so that there would be an overlapping of size ranges from basket to basket at each station. The number of oysters per basket ranged from sixty in the smaller size ranges to twenty in the maximum size group. All oysters were carefully culled and cleaned prior to the initial measurement, and on each measurement date thereafter any excessive growth of barnacles or young oysters was cautiously removed.

Complete monthly measurement data for each station is too extensive for inclusion here, but it is available in the files of the Florida State Board of Conservation and the Institute of Marine Science. For present purposes it is sufficient to show the initial and final measurement for all baskets (Table 6), and the mean monthly growth per basket at each of the two stations, Figure 4. Taking the total mean growth over the period of measurement as one hundred per cent, the cumulative per cent growth per month from all observations is shown in Figure 5.

Monthly mortality was noted by counting the boxes per basket on each measuring date. The monthly per cent mortality of both stations is shown in Figure 5.

e) *Spatfall*

Spatfall data is available from November 5, 1951 through February 20, 1952, and from June 3 through July 19, 1952. Observations were made at ten stations during

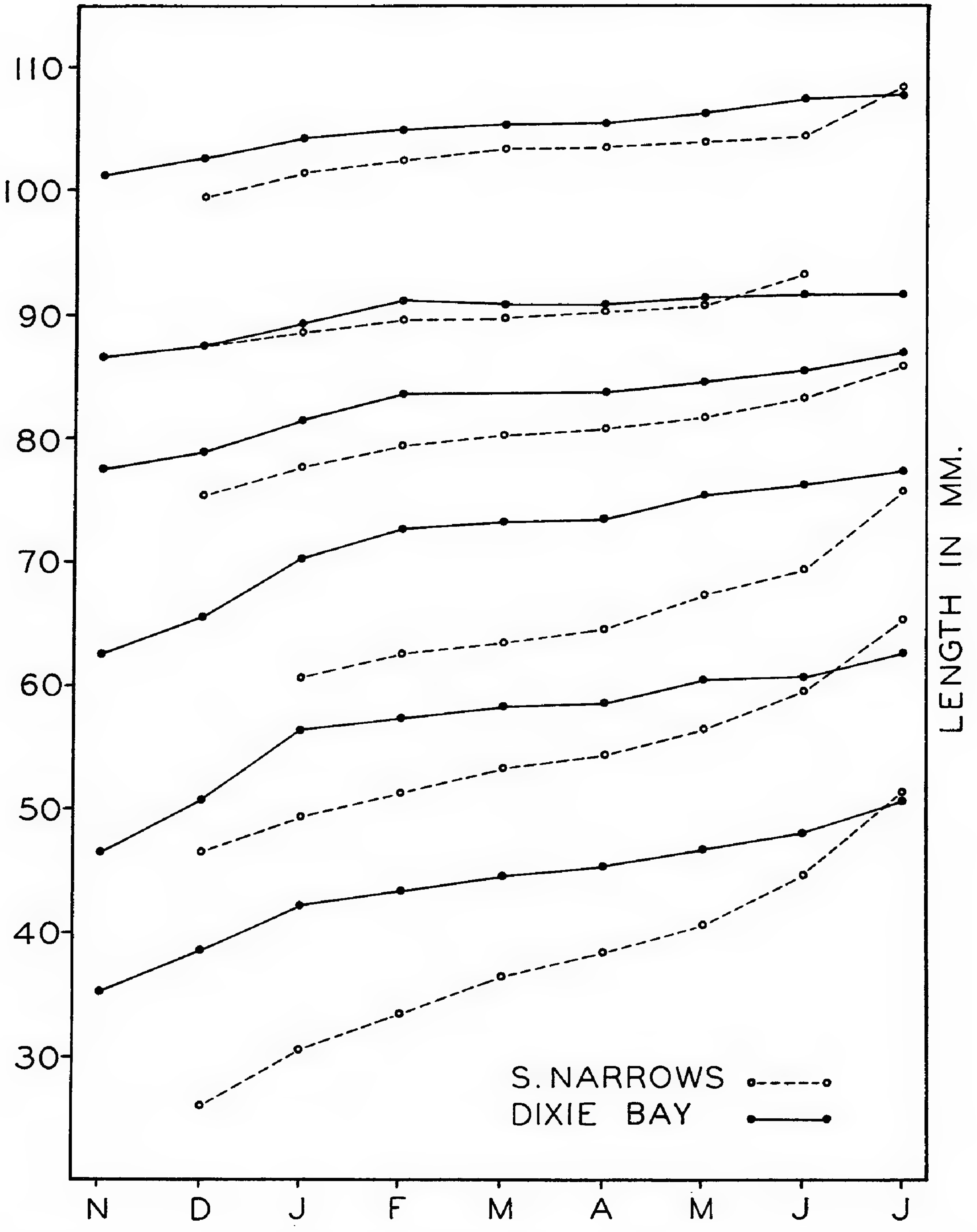

Figure 4. Mean monthly growth, per basket, at the Dixie Bay and South Narrows growth rate stations.

the first period and at eleven during the second. Spat collectors were placed on the bottom where they would not be exposed during low tides, and the stations selected were representative of both the backswamp and Crystal Bay areas.

No set was observed at the South Narrows, North Narrows and Dixie Bay stations during the Fall and Winter study. During the same period, however, spat were found setting at five of the Crystal Bay stations. With the exception of the period from Jan-

TABLE 6

Summary of initial and final measurement data, per basket, at each growth station.

Basket No.	Date	Size Range in mm.	Number Measured	Mean Length in mm.	Mean Increment in mm.
		DIXIE BAY			
1	11-21-51	12-44	60	35.3	......
1	7-23-52	32-67	47	50.6	15.3
2	11-21-51	36-57	58	46.4	......
2	7-23-52	52-79	39	62.8	16.4
3	11-21-51	50-73	60	62.6	......
3	7-23-52	67-90	53	77.1	14.5
4	11-21-51	70-93	60	77.8	......
4	7-23-52	73-106	51	87.0	9.2
5	11-21-51	77-101	25	86.8	......
5	7-23-52	80-108	23	91.8	5.0
6	11-21-51	91-132	20	101.2	......
6	7-23-52	93-141	16	107.9	6.7
		SOUTH NARROWS			
1	12- 5-51	13-38	36	26.0	......
1	7-11-52	31-70	29	51.3	25.3
2	12- 5-51	37-55	41	46.7	......
2	7-11-52	48-98	36	65.2	18.5
3	1- 5-52	48-76	59	60.8	......
3	7-11-52	61-98	53	75.9	15.1
4	12- 5-51	65-88	50	75.3	.. .
4	7-11-52	71-101	45	86.0	10.7
5	12- 5-51	76-102	24	87.4	......
5	6- 6-52	82-108	24	93.3	5.9
6	12- 5-51	84-115	25	99.7	......
6	7-11-52	95-124	25	108.3	8.6

TABLE 7

Maximum and total spat counts observed in both the Fall-Winter, and Summer Studies.

	FALL-WINTER			SUMMER		
Station	Number of Collectors	Max. Count	Total Count	Number of Collectors	Max. Count	Total Count
N. Dixie Bay	6	0	0	4	7	7
S. Dixie Bay	0	..	..	1	1	1
N. Narrows	6	0	0	4	4	4
S. Narrows	8	0	0	4	14	22
Shell Island	8	6	11	4	67	81
Marker #12	7	25	32	4	134	227
Marker #5	8	256	270	4	171	345
Mangrove Point	5	1	1	4	224	599
Mullet Key	6	2	3	3	20	42
Drum Island	4	0	0	4	343	502
Tin Pan Gap	1	0	0	4	100	127

uary 8th to 21st, at least one spat per twenty shells was found at Marker #5 until the termination of the Winter study. Throughout both periods the maximum observed set was three hundred and forty-three spat per twenty shell surfaces. This occurred at Drum Island during the twelve days preceding June 4th.

The maximum and total spat counts for each station are shown on Table 7. Maximum count refers to that of a single collector, whereas the total count represents the number of spat observed on all shells examined. The summer figures for the South Narrows station therefore mean that a total of eighty shells were examined from four collectors, that the greatest number of spat per collector was fourteen, and that a total of twenty-two spat were observed on the eighty shells.

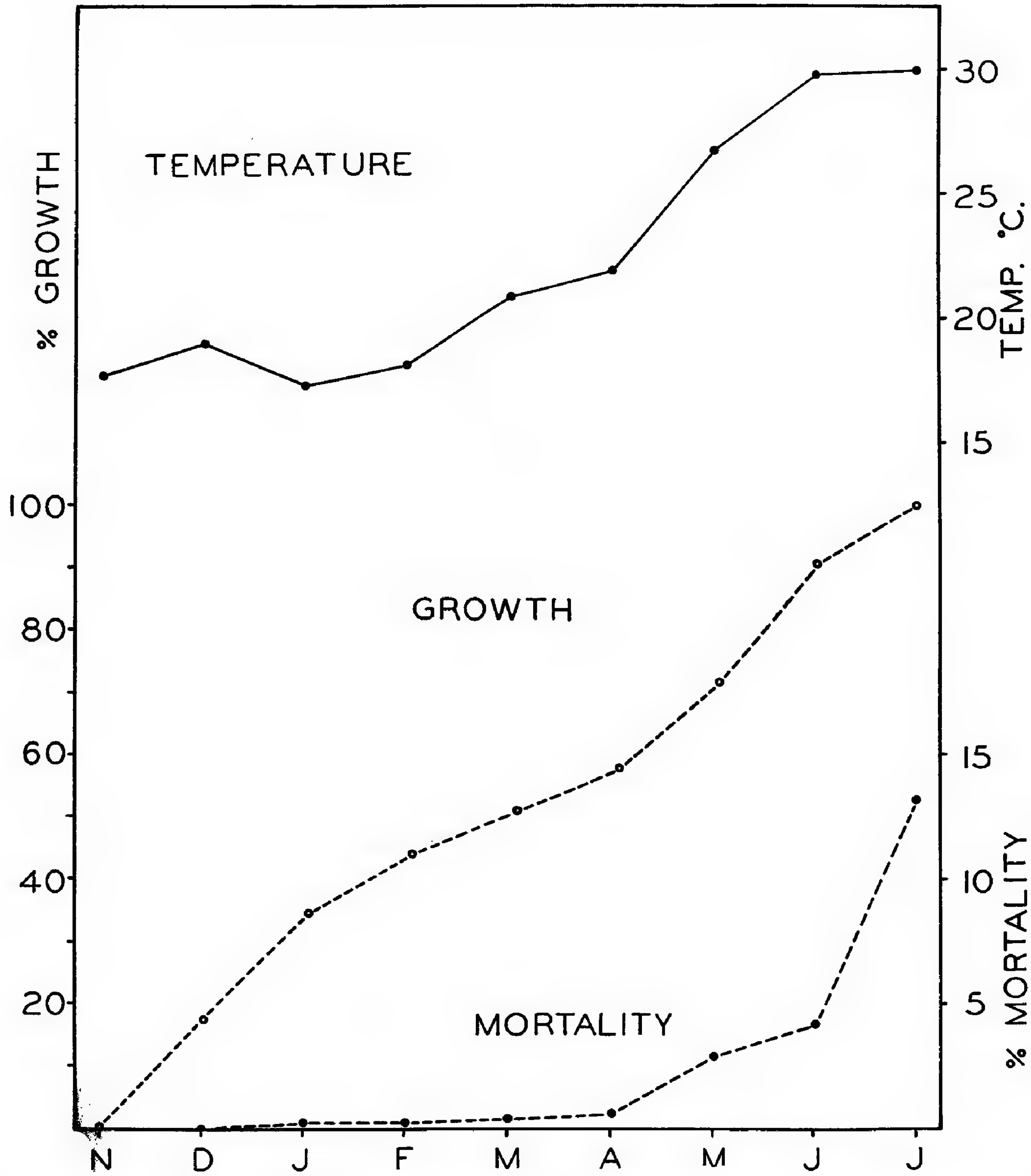

Figure 5. Mean Inverness air temperature, 1951–52; Cumulative per cent growth per month of all experimental oysters, and per cent mortality per month.

DISCUSSION

Compared with other estuarine or protected waters of the Florida west coast (Dawson, 1953, 1955a; Ingle and Dawson, 1950, 1953a) the Crystal River region is an area of low salinity. In addition to having the lowest mean salinity of any of the Florida oyster regions so far investigated, these waters generally exhibit minimal salinity variation. Reference to Tables 2 and 4 will show that during the 1951-52 period, the maximum observed salinity range at any station was 19.1 ‰, and maximum weekly and serial variations were 4.4 ‰ and 8.4 ‰ respectively. Although differences in area, depth, sources of fresh water, etc., prohibit a direct comparison of Tampa Bay and Apalachicola Bay salinities with those of Crystal River, it is worth noting that serial samples in Tampa Bay and Apalachicola Bay had maximum observed ranges of 14.1 ‰ and 17.7 ‰ and weekly salinity ranges in excess of 11.00 ‰ are not uncommon at Apalachicola. No comparable serial or weekly data are available for Cedar Keys but salinities there average above 20.0 ‰.

The Crystal River oyster grounds are naturally divided into two separate and distinct environments, the Salt River (backswamp) and Crystal Bay. In addition to the contrasting geographic features previously described, each exhibits separate salinity characteristics and differences are apparent in the oyster populations. Stations in the backswamp (Table 2, Big Coon Gap through S. Narrows) had an observed minimum salinity range of from 4.3 ‰ to 19.6 ‰; the mean salinity was roughly 12 ‰ and weekly variations averaged 1.6 ‰. Excepting the Coon Gap station, which is subject to wide variation due to its location in relation to the Crystal River and Crystal Bay, there is a general increase in maximum salinity as would be expected with increased distance from the Crystal River. In respect to minimum salinities, however, one will note a decrease from N. Dixie Bay to the low at the S. Narrows station. This is a reversal of expected conditions and, since no additional fresh water source is known, it probably indicates a northward flow of low salinity water from the Homosassa River system. Strong north-south currents, especially noticeable in the Narrows, are observed in the Salt River and their occurrence has been previously noted by Price (in press).

Considered as a whole, the oyster population of the backswamp is relatively small, but the individual oysters are normally large, well rounded, heavy shelled specimens. Coon oysters are comparatively scarce and the "mud oysters," common along the edge of the marsh, are well-cupped and possess sturdy shells. Fouling in this area is at a minimum as may be seen in Plate 2, and although there is some infection by *Polydora,* conchs or other predators are apparently excluded by the characteristically low salinities. The available data together with numerous observations on natural cultch shows that spatfall in the backswamp is exceptionally low. Since these bottoms are predominately of soft mud, natural cultch is at a premium and consists mainly of oyster shell. The deficient set of young oysters, together with a scarcity of cultch, effectively serves to keep the oyster population at a low level.

Situated between two river systems and subject to direct surface drainage from the surrounding uplands on the east, the backswamp oyster population is further threatened by flood conditions during hurricanes or abnormally wet years. At such times salinities are doubtless reduced to the minimum. Verbal reports of local inhabitants concerning mortalities of Salt River oysters following the 1950 hurricane season are in conformity with this observation.

In general, therefore, the oyster population of the Crystal River backswamp area closely approximates the first category of Gulf oyster communities characterized by Butler (1954). Salinity averages higher than the 10 ‰ suggested by Butler may possibly account for the better quality oysters. Despite this seemingly precarious habitat of the Salt River oysters these stocks have long been subject to the predations of man. Numerous Indian shell mounds are found throughout the Narrows and today the Crystal River fishery is generally restricted to this area until December or January of each year.

Located between the Salt River and Crystal River is a broad transition zone on which there are little data. Here there are numerous coon bars of considerable extent, and commercial oysters are found only occasionally in the inter-island channels or in a few holes, two to three feet deep. The Mullet Key area on the western margin of this zone supports a population of two to two and a half inch round, thick shelled oysters which consistently fail to show any external evidence of growth.

Omitting for the present Shell Island and Salt River Branch, both within the Crystal River, all the remaining stations are located within Crystal Bay. The maximum observed salinity range in this region was from a low of 3.2 ‰ at Marker # 16 to 28.4 ‰ at Marker #5; the mean salinity was roughly 16 ‰ and weekly variation averaged 3 ‰. Salinity data from the southern limit of the area, Mangrove Point, show little evidence of dilution by waters from the Homosassa River complex. To the north, however, the reduced maximum and minimum observations at Drum Island, compared with those at Demory Gap and Tin Pan Gap indicates that the Withlacoochee River lowers the salinities in the northermost waters of the study area. The Withlacoochee is a relatively large stream and under flood conditions can be expected to influence salinities at least as far south as Tin Pan Gap. The duration and magnitude of such reductions cannot be estimated from the data available.

Unlike many estuarine areas where comparatively continuous depth and current gradients may obtain, Crystal Bay is interspersed with numerous oyster and shell reefs rising abruptly from the surrounding bottom. Each of these acts as a baffle and accordingly serves to deflect the otherwise normal flow of water. This condition is most apparent during the lower tide stages, but the effects are continuous throughout the tidal cycle. While the reefs have a gross north-south orientation, individual segments have developed all shapes and orientations. In one instance a bar several hundred yards long has formed an almost complete oval, comparable to an atoll, and except during high tide stages the waters within are essentially stagnant.

Current patterns throughout the area are extremely confused and fluctuate widely during any period of observation. Because of these conditions, it is impossible from the available data to arrive at definite conclusions regarding the mixing or distribution of Crystal River water after it passes Shell Island. However, the data do suggest a northerly inshore deflection past Black Point and Negro Island, and a general inshore-offshore salinity gradient is apparent along the channel stations.

Although subject to greater fluctuations than those of the Salt River area, the salinities of Crystal Bay are very stable when compared with those of the other oyster regions of Florida. Wide variation may occur during flood years, but such conditions are abnormal.

Water temperature here as well as those of the backswamp waters are within the range observed at Apalachicola (Dawson, 1955a).

Crystal Bay oysters are generally restricted to the immediate vicinity of the reefs or high bars, and at least three main types of oysters may usually be found in a single locality. Clumps of small and densly clustered coon oysters cover or fringe the reef crown; below these and extending to near the base of the reef grow clusters of narrow, thin-shelled, scissor-bills and these are interspersed with a small number of moderately heavy shelled, single or double, oysters of good quality. Commercial quality oysters are more numerous within the reef gaps and such areas are heavily exploited by the oystermen. Oysters in such localities, however, frequently suffer from high mortalities of unexplained cause. Mortalities do not strike all the gaps in a reef or a reef complex but appear to occur haphazardly. Evidence of good growth rate was seen by general observation on all stocks, excepting the predominately exposed coon oysters.

As previously shown, isolated spat were setting in Crystal Bay as late as February 1952, and at least during the months of June and July a commercially significant set occurred in the area. Total spat per station, approaching the Apalachicola Bay maxima (Ingle, 1951) were not observed.

Moderate barnacle fouling occurs in the area, but this was seldom found sufficiently abundant to be detrimental to oyster growth or setting. Few conchs, either *Thais* or *Melongena*, were observed and a moderate percentage of oysters was infected with *Polydora* and *Cliona*. Although not observed by the author, it was reported by the oystermen that "all oysters on the bars between Tin Pan Gap and the Withlacoochee River" are periodically killed by the "leech," presumably *Stylochus frontalis*. It could not be determined whether the "leech" was actually observed by the oystermen, and there is a possibility that such mortalities could be the result of other causes such as *Dermocystidium marinum* infections.

The Crystal Bay oyster population closely approximates the characteristics of Butler's (1954) second category of Gulf oyster communities, that with an annual salinity mean of 15‰.

Results of concurrent surface-bottom salinity sampling (Table 4) show the presence of a slight "salt wedge" effect in the Crystal River and channel at least as far upstream as the Salt River Branch, where the means of fourteen observations showed bottom salinities to be 0.3 ‰ higher than those of the surface. At this station, however, surface salinities on four occasions exceeded those at the bottom up to a maximum of 2.4 ‰. This is not an unusual occurrence in Gulf estuarine waters as indicated by Gunter (p. 19, 1945), who reported salinity inversion in six of one hundred and nine observations. Gunter's findings were in the open, wind-swept waters of the Texas bays and probably were, as he suggested the result of turbulence.

The Salt River Branch is deep, approximately fifteen feet at MLW, and well protected, and it is doubtful whether turbulence alone can account for the present observations. Salinity inversions occurred on both the ebb and flood; no correlation is noted with existing wind conditions, and corresponding salinities at Coon Gap were not abnormally high. Two possible explanations occur; one is that there were short term increases in the flow of nearby springs, or that a decrease in river discharge permitted the influx of more saline surface waters from Coon Gap. A complete analysis of this problem would require more detailed data than is presently available.

Studies on the Dixie Bay and South Narrows growth rate (Table 6, Figures 4 and 5) show that growth occurred throughout the study period. Rapid growth was recorded during December, January and June, and this accounted for more than sixty per cent of the observed increment. Minimum growth occurred during March and April and probably corresponded with onset of a spring peak of spawning. Unfortunately, I have no spatfall data for this period. Water temperatures during this period were generally above the minimum required for oyster growth and no unusual salinity conditions were recorded.

Maximum period growth was in Basket #1 at South Narrows, where the mean length increased 25.3 mm, from 26.0 mm to 51.3 mm. This is equivalent to an average weekly increment of 0.8 mm. Maximum observed weekly growth was 1.3 mm in oysters averaging 76 mm.

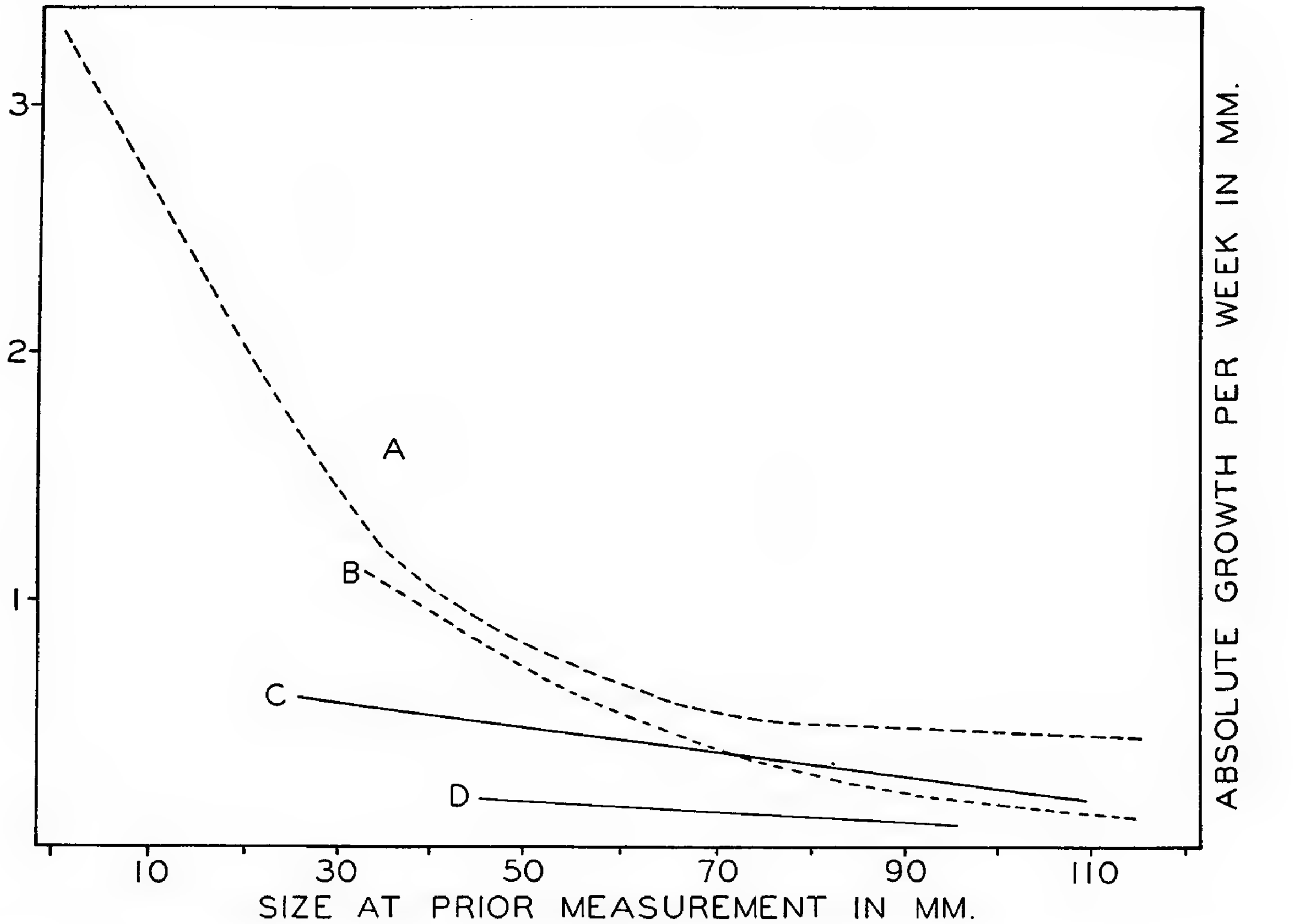

Figure 6. Comparative growth rates at four Florida localities: *A*—Apalachicola Bay; *B*—Tampa Bay; *C*—Crystal River; *D*—Cedar Keys.

It is apparent that although the growth for the experimental oysters was moderately rapid, it cannot compare with the 2.0 mm to 4.2 mm weekly increments reported by Ingle (1950) for Apalachicola oysters of similar size. Neither did it approximate the mean daily growth of 0.3 mm observed by Gunter (1951) for oysters growing in the open Gulf off Barataria Pass, Louisiana.

With the inclusion of present data, estimates of the expected growth rates of Florida oysters are available from four west coast localities and are shown in Figure 6. Minimum growth may be expected at Cedar Key (Ingle and Dawson, 1953a), and the growth rates at Tampa (Dawson, 1953) and Crystal River are similar, at least in the larger size ranges. It will be noted that none of the curves approximate that shown of Apalachicola. For oysters in excess of 80 mm long the expected growth rates do not approach that based on the Apalachicola studies (Ingle and Dawson, 1953b). Decrease in growth rate is to be expected with increased size and the Apalachicola data probably illustrates extreme or even abnormal growth for large oysters.

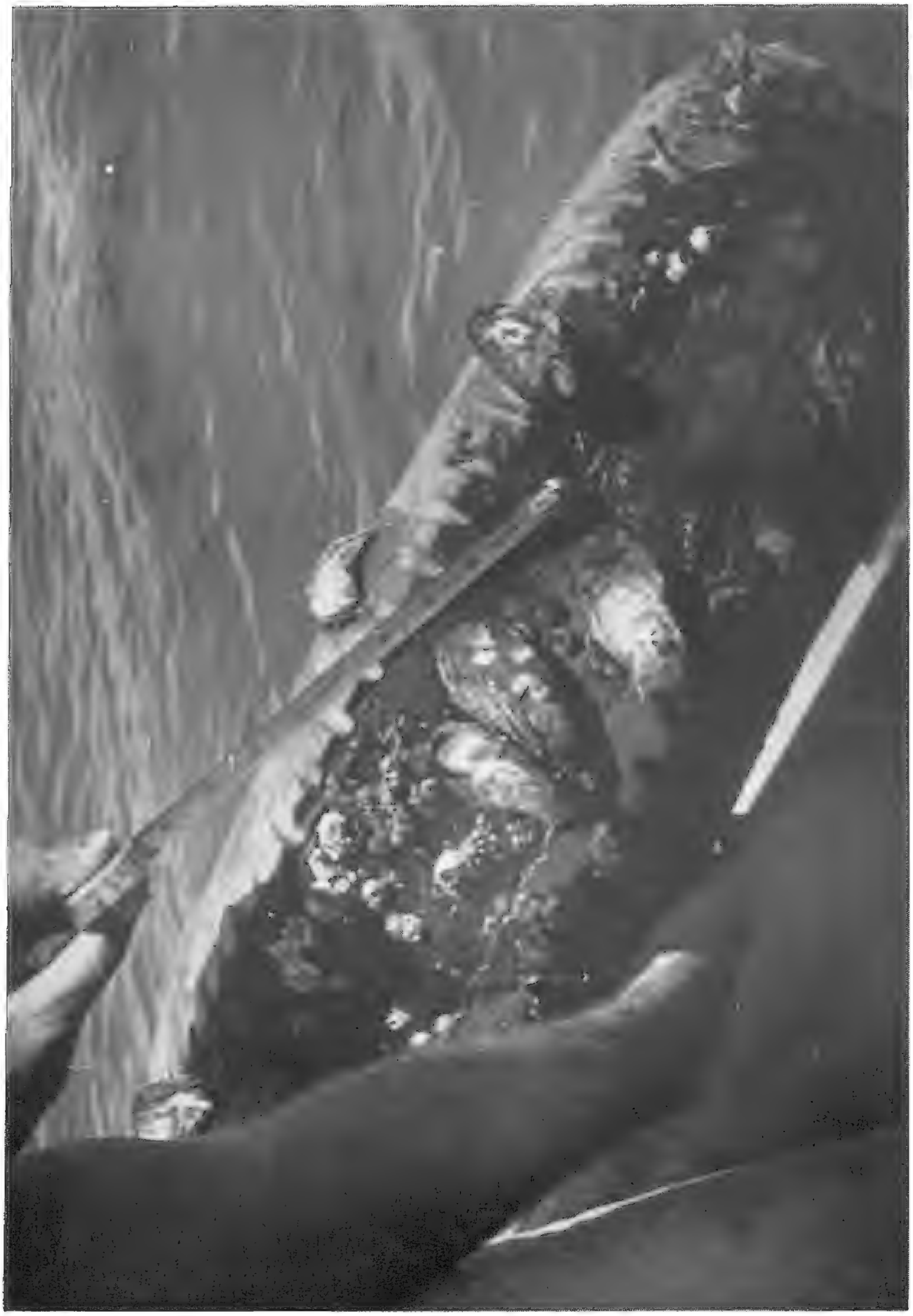

Plate 2. Oysters grown in Dixie Bay in less than one year; largest individual approximate 3.5 inches long.

Although no studies were made at Crystal River on growth rate from setting to commercial size, the oysters shown in Plate 2 were grown in approximately one year. This tire was set out in Dixie Bay about August 1, 1952 and was photographed on or about July 15, 1953. The oysters and fouling shown constitute the total surviving set and fouling, for the tire was not culled or cleaned prior to being photographed. These oysters were the largest found on several tires which had been out for the same period, and the largest individual was approximately three and a half inches long. Minimum daily growth for this individual was roughly 0.25 mm and approximates the 0.3 mm daily increment noted by Gunter (1951). This is equivalent to growth from set to market size in a year's time, and such is commonly experienced on the Gulf coast under favorable conditions. This is probably about the peak rate which Gulf oysters maintain for an extended period.

Mortality data is limited to that accruing during the growth rate study, and no estimate of the natural mortality of the area is available. Per cent mortality per month (Figure 5) ranged from zero to the maximum of 13.2% in July; cumulative mortality over the period was 21.2%. No correlation was found between salinity variation and mortality, but close correspondence is noted between increased temperature and increased mortality. The study terminated early in the summer and total mortality shown above cannot be considered as representative for the region. It is not improbable that high mortality continued until the approach of cooler temperatures in October.

Increased mortality with increased temperature has previously been noted in both the Gulf and Chesapeake Bay (Mackin, 1951; Collier, 1953; Hewatt and Andrews, ·954). It has been suggested by Collier (1953) that mortalities are not caused by high temperatures *per se,* but that under conditions of high temperature, above 25° C., oysters are more susceptible to attack by predators and parasitic infections. Mackin (1951) has shown the optimum temperature for the development of *Dermocystidium marinum* in Louisiana to be about 22° to 25° C.

At Crystal River water temperatures in excess of 22° C. were experienced late in April, and a pronounced increase in mortality occurred thereafter. *D. marinum* is known to occur in Florida and in fairly low salinity waters (Dawson, 1955b) and this parasite might be responsible for the high summer mortality experienced at the Crystal River localities, but no data are available.

SUMMARY

The Crystal River is a clear spring-fed stream discharging into the Salt River, a backswamp or marsh region, and also into Crystal Bay, which is merely an indentation of the Gulf of Mexico, with oyster bars delimiting the seaward side.

A series of unprotected oyster reefs extend up to three and a half miles into the Gulf of Mexico off the mouth of the Crystal River. Roughly parallel to the coast, the north-south extent of these reefs is approximately thirteen miles.

The area experiences a mean annual air temperature of approximately 71° F., with maximum temperatures occurring during July and August and minima in December and January. Total annual precipitation is roughly fifty inches, of which more than sixty per cent occurs from June through September.

Salinity characteristics are estuarine. Mean salinities are lower than at any of the other Florida oyster regions previously investigated, and long and short term variations are minimal. Salinities of the backswamp ranged from 4.3‰ to 19.6‰, and weekly variations averaged 1.6 ‰. Crystal Bay salinities ranged from 3.2 ‰ to 28.4 ‰ with an average weekly variation of 3.0 ‰. Mean salinities for the two areas were approximately 12 ‰ and 16 ‰, respectively. Water temperatures were within the range found in other Florida estuaries.

A slight "salt wedge" effect was observed in the Crystal River and unexplained inversions, with higher salinity at the surface, were recorded at the Salt River Branch.

Oyster populations of the backswamp were small but individual oysters were of high quality. Three main types of oysters were observed in Crystal Bay and their distribution noted. These are coon oysters, clusters of narrow scissor bills and well formed, heavy shelled, commercial grade oysters. Isolated and unexplained mortalities occur in this area.

Spatfall was exceptionally low in the backswamp. A commercially significant set was observed in Crystal Bay during June and July, and isolated spat were setting as late as February. Observed set was not comparable to the maxima reported for Apalachicola Bay.

Experimental studies indicate rapid growth in the area, but it does not approach that of Apalachicola Bay oysters. Growth rates at four Florida localities are compared. An instance of growth from spat to commercial size within a year is described from Dixie Bay.

Increased mortality was found to accompany increasing temperature.

REFERENCES

Butler, Philip A. 1954. Summary of our knowledge of the oyster in the Gulf of Mexico. U. S. Fish Wildl. Serv., Fish. Bull. 89: 479–489.

Collier, Albert. 1953 (1954). A study of the response of oysters to temperature, and some long range ecological interpretations. Convention Addresses Natl. Shellfisheries Assoc. 1953: 13–38, figs. 1–8 (Processed).

Davis, J. H., Jr. 1940. The ecology and geologic role of mangroves in Florida. Carnegie Inst. Wash. Pub. 517, Pap. Tortugas Lab. 32(16) : 303–412, figs. 1–7, 12 pls.

Dawson, C. E. 1953. A survey of the Tampa Bay area. Fla. State Brd. Conservation, Tech. Series. No. 8: 1–39, Figs. 1–13.

———— 1955a. A contribution to the hydrography of Apalachicola Bay, Florida. Publ. Inst. Mar. Sci. (Univ. Texas) 4(1) : 13–35.

———— 1955b. Observations on the incidence of *Dermocystidium marinum* infection in oysters of Apalachicola Bay, Florida. Texas Jour. Sci. 7(1) : 47–56, 1 fig.

Ferguson, G. E., C. W. Lingham, S. K. Love, and R. O. Vernon. 1947. Springs of Florida. Fla. Geol. Surv. Geol. Bull. 31: 1–196, figs. 1–37, 1 map.

Florida State Board of Conservation. 1948. Observed rainfall in Florida; monthly totals from beginning of records to 31 Dec., 1947. Fla. State Brd. Conservation, Divn. Water Surv. Res. 427 pp., 31 maps.

Greer, B. F. 1954. Summary of Florida commercial marine fish landings for 1953. Rept. Mar. Lab., Univ. Miami, pp. 1–28 (mimeo.).

Gunter, Gordon. 1945. Studies on marine fishes of Texas. Publ. Inst. Mar. Sci. (Univ. Texas) 1(1) : 1–190, figs. 1–11.

———— 1951. The West Indian tree oyster on the Louisiana coast, and notes on growth of the three Gulf Coast oysters. Science, 113 (2940) :516–517.

Hewatt, Willis G., and Jay D. Andrews. 1954. Oyster mortality studies in Virginia. I. Mortalities of oysters in trays at Gloucester Point, York River. Texas Jour. Sci. 6(2) :121–133, figs. 1–5.

Ingle, R. M. 1950. Summer growth of the American oyster in Florida waters. Science, 112(2908) : 338–339.

——— 1951. Spawning and setting of oysters in relation to seasonal environmental changes. Bull. Mar. Sci. Gulf Caribb. 1(2): 110–135, figs. 1–3.

Ingle, R. M., and C. E. Dawson. 1950 (1951). Variations in salinity and their relations to the Florida oyster. Salinity variations in Apalachicola Bay. Proc. Gulf Caribb. Fish. Inst. 3: 35–42, figs. 1–6.

——— 1953a. A survey of the Cedar Key area. Fla. State Brd. Conservation, Tech. Series. No. 9: 1–27, figs. 1–11.

——— 1953b. Growth of the American oyster, *Crassostrea virginica* (Gmelin) in Florida waters. Bull. Mar. Sci. Gulf Caribb. 2(2): 393–404, figs. 1–7.

Lunz, G. Robert. 1951. A criticism of oyster measurements. Proc. Gulf Caribb. Fish. Inst. 4: 48–49.

Mackin, J. G. 1951 (1953). Incidence of infection of oysters by *Dermocystidium* in the Barataria Bay area of Louisiana. Convention Addresses Natl. Shellfisheries Assoc. 1951: 22–35. (Processed.)

Marine Laboratory, University of Miami. 1952. Recapitulation of 1951 Fish census. Rept. to Fla. State Brd. Conservation, pp. 1–32 (mimeo.).

Price, W. Armstrong. 1954a. Shorelines and coasts of the Gulf of Mexico. U. S. Fish Wildl. Serv., Fish. Bull. 89: 39–65, figs. 12–15.

——— 1954b. Oyster reefs of the Gulf of Mexico. U. S. Fish Wildl. Serv., Fish. Bull. 89: 491.

——— (in press) Low energy coast and its new shoreline types on the Gulf of Mexico. Comm. IV Congrès INQUA (Internatl. Assoc. Quarternary Res.), 1953, Rome and Pisa, Italy.

Ruge, John G. 1898. The oysters and oyster beds of Florida. Bull. U. S. Fish. Comm. 17: 289–296.

Stauber, L. A. 1943. Graphic representation of salinity in a tidal estuary. Jour. Mar. Res. 5(2): 165–167, 1 fig.

U. S. Coast and Geodetic Survey. 1949. United States Coast Pilot, Gulf Coast, Key West to Rio Grande. 3rd ed., 505 pp., U. S. Dept. Commerce Ser. No. 725; Chart No. 1258.

U. S. Fish and Wildlife Service. 1952. Florida Landings. Issued monthly.

——— 1953. Fishery statistics of the United States 1950. Statist. Dig. U. S. Fish Wildl. Serv. 27: 1–492.

U. S. Weather Bureau. 1955. Climatic summary of the United States—Supplement for 1931 through 1952; Florida, No. 6, 35 pp.

Vernon, R. O. 1951. Geology of Citrus and Levy counties, Florida. Fla. Geol. Surv. Geol. Bull. 33: 1–256, figs. 1–40, 2 maps.

Visher, Stephen S. 1954. Climatic Atlas of the United States. 403 pp. Harvard University Press, Cambridge, Mass.

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PORT ARANSAS, TEXAS

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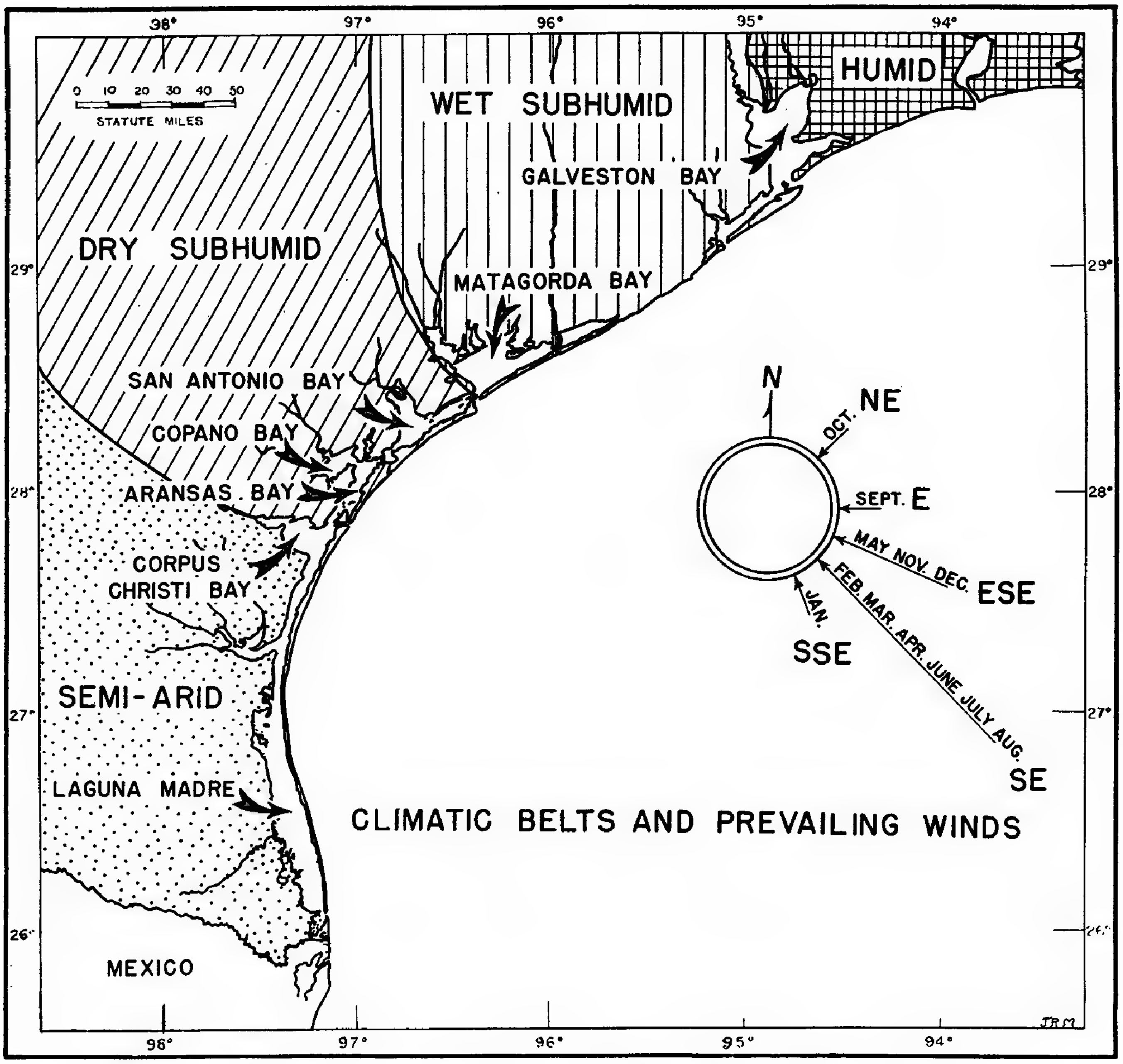
Texas Bay Sediments[1]

Francis P. Shepard and Gene A. Rusnak

Introduction

With the help of an American Petroleum Institute grant, a group of Scripps Institution scientists have been investigating the sediments of Texas bays during the past six years. In many respects these bays have proven ideal for a study of sedimentation. In the first place, with the climatic zonation found between the Louisiana border to the northeast and Laguna Madre to the southwest (Fig. 1), it has been possible to study the dif-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STATUTE MILES
HUMID
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GALVESTON BAY
DRY SUBHUMID
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29°
SAN ANTONIO BAY
COPANO BAY
ARANSAS BAY
28°
CORPUS CHRISTI BAY
SEMI-ARID
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LAGUNA MADRE
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SE
CLIMATIC BELTS AND PREVAILING WINDS

Fig. 1. Index chart of Texas coast, showing climatic belts (after Thornthwaite, 1948) and prevailing wind directions (after Lohse, 1955).

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[1] Contribution from the Scripps Institution of Oceanography, New Series No. 932. This investigation was supported by a grant from the American Petroleum Institute, Project 51.

ferences between sediments in bays of a humid area and those in areas of semiaridity. Streams provide large amounts of sediment to the bays in the humid areas, whereas windblown sands and washovers from the barrier islands provide the principal source for the semiarid bays. The differences in salinity in the bays, ranging from over 80‰ in Laguna Madre to approximately 1‰ at the mouths of some of the rivers entering the bays to the north, have a tremendous effect on the organisms and on the nature of sedimentation as it is related to these organisms. A second advantage of studying the Texas bays is that they are closed off from the open Gulf by almost continuous barrier islands so that sediments are more likely to be permanent than in open bays where sediments are often deposited and then removed by marine processes. Borings have shown that these bay sediments are present well below the bay bottoms. A third advantage of the Texas area to a student of sedimentation comes from the very complete surveys made by the U.S. Coast and Geodetic Survey around 1870 and again around 1934. These surveys provide a means of determining roughly the rate of sedimentation as related to other factors (Shepard, 1953).

It was thought at first that a very complete study should be made of the bays in the vicinity of Rockport, particularly San Antonio Bay into which the Guadalupe River enters. This has been done (see bibliography at end). It was realized, however, after some time had been spent on these concentrated studies, that a much better understanding of bay sedimentation in general and of the processes which contribute to it would come from making comparisons with other bays along the Texas coast. This became particularly evident when some rather large contrasts were found betweeen the sediments of the Laguna Madre, which is located in a semiarid climate and has virtually no entering streams, and the sediments of San Antonio Bay with its dry sub-humid climate, its entering streams, and its extensive oyster reefs. Furthermore, the importance of inlets on sedimentation soon became evident because tidal currents transport sediments into the bays from the barrier islands and from the shallow portions of the Gulf of Mexico.

In order to obtain some idea of the nature of Texas bay sedimentation, it is important to consider in some detail the characteristics which bays of these two contrasting types possess. Thus some description will be made of the bays of the Rockport-Aransas Pass area, especially San Antonio Bay, and of the Laguna Madre.

Rockport-Aransas Pass Area (San Antonio Bay)

Located almost in the center of the Texas coast, San Antonio Bay has many of the characteristics of the subhumid type of bay found along the coast from Corpus Christi to Galveston. The accompanying chart (Fig. 2) shows that, with the exception of oyster reefs, topographically this bay has only very minor bottom irregularities and is very shallow. In few places does it reach depths greater than six feet. To the north it is influenced by the Guadalupe River. At the present time this river flows into the isolated arm of the bay north of the delta, although in the not distant past it was entering directly into the upper San Antonio Bay through a series of channels cutting across the delta. The salinity, ranging under average conditions from about 4‰ at the northern end to about 25‰ at the southern end, shows fluctuations both seasonally and periodically because of the effect of drought on the one hand, and of floods on the other. A tongue of low salinity extends down the west side of the bay, whereas a tongue of relatively high salinity, ap-

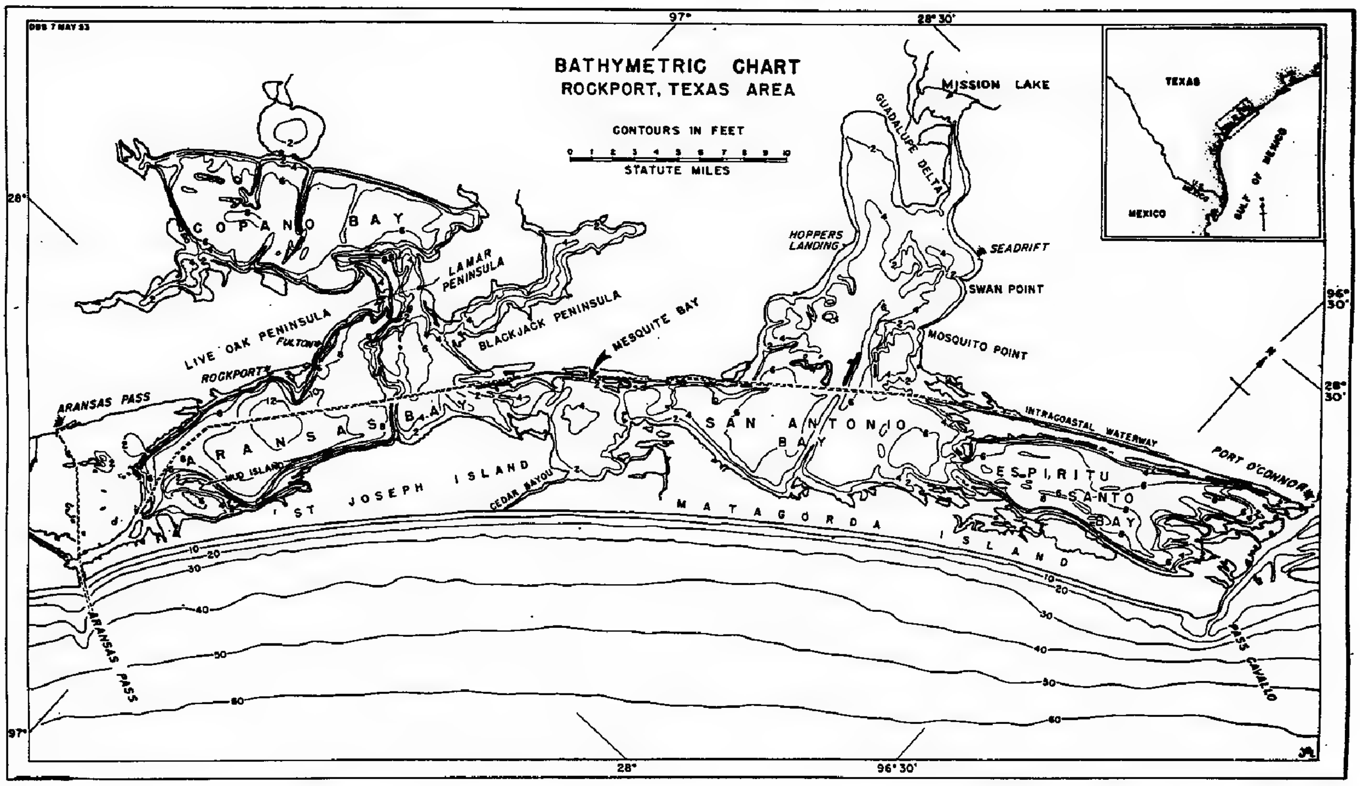
BATHYMETRIC CHART
ROCKPORT, TEXAS AREA
CONTOURS IN FEET
STATUTE MILES
97°
28°30'
MISSION LAKE
GUADALUPE DELTA
HOPPERS LANDING
SEADRIFT
SWAN POINT
MOSQUITO POINT
INTRACOASTAL WATERWAY
PORT O'CONNOR
TEXAS
MEXICO
GULF OF MEXICO
96°30'
28°30'
COPANO BAY
LAMAR PENINSULA
BLACKJACK PENINSULA
MESQUITE BAY
LIVE OAK PENINSULA
FULTON
ROCKPORT
ARANSAS PASS
ARANSAS BAY
SAN ANTONIO BAY
ESPIRITU SANTO BAY
ST JOSEPH ISLAND
CEDAR BAYOU
MATAGORDA ISLAND
ARANSAS PASS
PASS CAVALLO
10
20
30
40
50
60
28°
96°30'
97°
28°

FIG. 2. Bottom topography of Rockport bays and nearshore area (after Shepard and Moore, 1955). Bay contour interval 2 feet. Offshore contour interval, 10 feet.

parently coming in through Espiritu Santo Bay, extends up the east side of San Antonio Bay. Oyster reefs are most numerous in the central portion of the bay where they rise almost to or actually to the surface.

The barrier island, consisting largely of sand, contributes some sediment to the southern area as the result of wind action, although this does not appear to be very important, partly because much of the northern portion of Matagorda Island is marshy and has marsh vegetation which largely prevents the movement of the sand from the dunes farther south. A rather important source of sand comes into the adjoining Mesquite Bay through the small intermittent Cedar Bayou Inlet and elsewhere by washover storm waves. Also, during northers, rather strong currents come down Espiritu Santo Bay and carry sand into the southern portion of San Antonio Bay.

The result of these influences is seen on a map showing the general sediment types, as based on sand, silt, and clay contents[2] along with the oyster reefs (Fig. 3). Here we see that in the area around the delta the sediments are dominantly clayey with considerable silt, and a tongue of equally fine sediment extends down the center and west side of the bay as does the current of low salinity water mentioned previously. Very sandy sediments mixed with clay are found in Mesquite Bay to the southwest where the effect of the inlet and washovers seems to be very important. This is also true of southeast San Antonio Bay near Espiritu Santo Bay where, because of the locally shallow depths and currents due to occasional strong northeast winds, the sediments are relatively high in sand.

Examination under the binocular microscope of different sieve sizes of the sandy fraction of these sediments indicates other important characteristics of the sediment zones. Thus the sediments near the delta, and particularly those near the mouths of the present streams, have rather high content of wood debris. Furthermore, mica is more

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[2] Dividing lines between sand and silt sizes are placed at 1/16 mm. and between silt and clay at 1/250 mm.

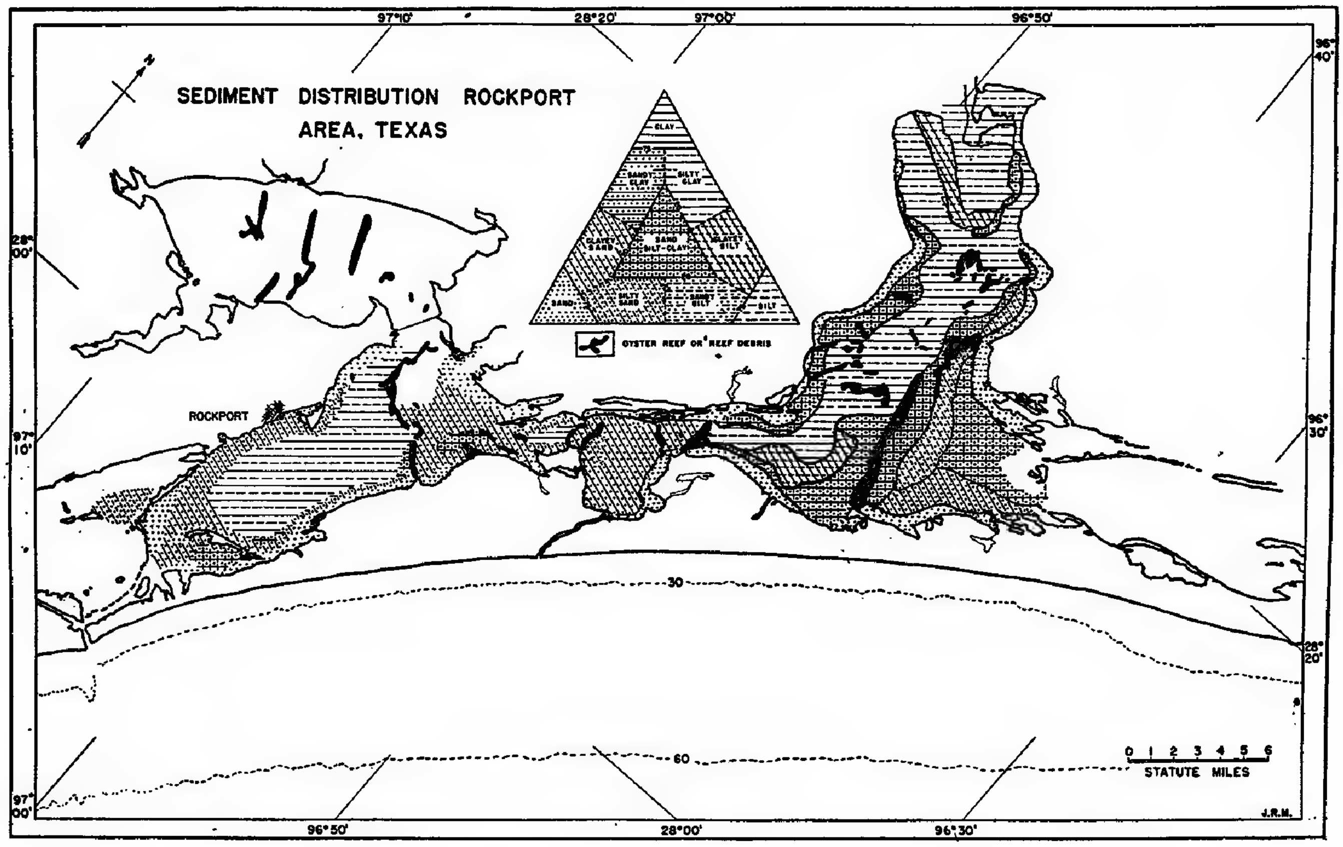
SEDIMENT DISTRIBUTION ROCKPORT AREA, TEXAS
97°10'
28°20'
97°00'
96°50'
96°40'
28°00'
97°10'
96°30'
28°20'
97°00'
96°50'
28°00'
96°30'
ROCKPORT
CLAY
SANDY CLAY
SILTY CLAY
CLAYEY SAND
SAND SILT-CLAY
CLAYEY SILT
SAND
SILTY SAND
SANDY SILT
SILT
OYSTER REEF OR REEF DEBRIS
30
60
0 1 2 3 4 5 6
STATUTE MILES
J.R.M.

FIG. 3. Sediment distribution in Rockport area bays based on sand-silt-clay content (after Shepard and Moore, 1955).

abundant in these areas than elsewhere. There are also small ferruginous aggregates. Each of these constituents becomes negligible in the sediment farther down the bay, away from the influence of the river. In addition the cores of the sediments in the vicinity of the delta show occasional lamination, whereas farther down the bays the cores are rarely if ever laminated. The reason for this contrast in sediment structure is that the sediments around the river mouths are being deposited rapidly and they are not much disturbed by the burrowing activity of benthonic organisms, most of which cannot tolerate low salinities. On the other hand, at a position away from the delta where there is a much greater abundance of these bottom dwellers, the bottom becomes churned and stratification has little chance to be preserved. In the portions of the bays where sand is being introduced through inlets, there is a very crude type of stratification due to the alternate introduction of sandy sediments, on the one hand, and of clayey sediments, on the other. Because of the burrowing organisms, however, this alternation is not exhibited by good stratification.

Borings made into San Antonio Bay a few years ago (Shepard and Moore, 1955, pp. 1546–1576) showed that the characteristic sediments of the present day persist in many places to depths of as much as 50 or even 80 feet below the bottom. Some borings extended down through unstratified clayey material as much as 50 feet, and elsewhere oyster reefs were penetrated continuously for as much as 40 feet. Similarly, borings in the sandy barrier islands which border San Antonio and other bays along this part of the coast, show that the sand continues with very little change in character to depths of as much as 50 feet. The study of the sediments from these borings has indicated quite clearly that deposition has continued over a long period, probably as much as 9,000 years judging from carbon 14 dates, with conditions very similar to the present. This can mean simply that sandy barrier islands developed at an early stage during the rise in sea level that accompanied the melting of the great glaciers some 10,000 years ago (Flint, 1953). These islands caused an early development of the lagoons and estuaries so that bay sedimentation has probably occurred continuously over these long periods. If the barrier islands had not developed at this early stage and instead had been formed recently, the sediments under the bays would be far sandier than they are because open Gulf shelf deposits formed at shallow depths in this area contain a high percentage of sand. Also the free access of Gulf waters would undoubtedly have brought in an abundance of echinoids, which are so characteristic of the continental shelf deposits on the outside and are so rare in bays. Virtually no echinoid plates or spines have been found in these borings beneath San Antonio Bay. Glauconite also develops characteristically in the sediments of the open Gulf and it is virtually missing in the bays and in the borings made into the bays. Indications are that the present barrier islands have changed only slightly in position from time to time during their upgrowth.

Laguna Madre

The Laguna Madre is a linear coastal lagoon extending for approximately 120 miles south from Corpus Christi Bay almost to the Mexican border. This lagoon is mostly very shallow and a large portion, especially in the center of the bay, is rarely covered by water (see Figure 4). The Laguna Madre has very different conditions than those of San Antonio Bay. There are no streams of any consequence entering the bay at the present time, although in the past the southern end of the bay has been supplied from time to time with the waters of the Rio Grande. Also during the occasional heavy rains the Arroyo Colorado and the small streams coming into Baffin Bay estuary near the northern end provide large quantities of fresh water which radically reduces the salinity for short periods. Although the floods do not affect salinity very long they must discharge much clay into Laguna Madre. Ordinarily, however, the high evaporation in the bay maintains a high salinity commonly greater than that of the open Gulf except near the inlet at Port Isabel. The absence of large supplies of sediments introduced by streams is counteracted by a very considerable source of sediment from Padre Island. This island, because of the greater aridity of the climate here than to the north, is much less covered with vegetation and during wind storms great quantities of sand are brought into the Laguna. Furthermore, the occasional rises in sea level that accompany hurricanes, or to varying degrees nearby hurricanes, send large quantities of sands from the barrier island into the bay through a series of low passes developing washover fans. However, this source of sand would soon be exhausted were it not for continual replenishment from the Gulf by sediment transport of coastal sand by longshore currents (Bullard, 1942, pp. 1021–1044; Lohse, 1955, pp. 99–105).

As a result of these influences, the sediments in Laguna Madre are quite different from those of the more humid bays to the north. Figure 4 shows that sand forms a much larger constituent of the sediments. Although we have not sampled the central exposed area of the bay, sand is said to be prevalent in this area with dunes building over on the mud flats which are only occasionally flooded by the lagoon waters. The only area where clay (more than 75% clay sized material) is found is in the central part of the relatively deep Baffin Bay, which is somewhat deeper than San Antonio Bay. Elsewhere relatively deep areas with silty clays, sand-silt-clays, and clayey or silty sands occur in the northern Laguna, Baffin Bay and in the southern part of the Laguna (See Fig. 4). Much of the

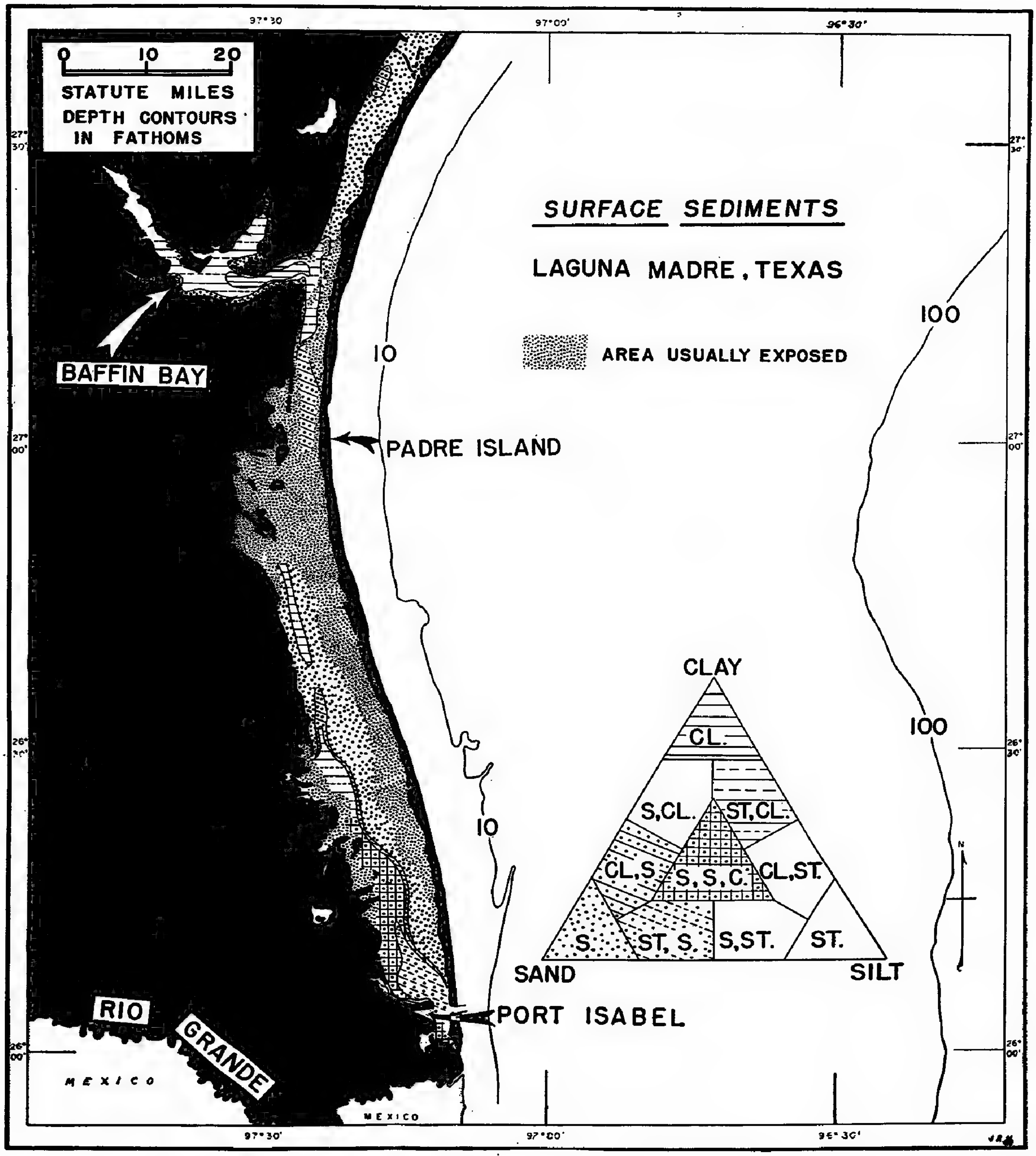
97°30'
97°00'
96°30'
27°30'
27°00'
26°30'
26°00'
0 10 20
STATUTE MILES
DEPTH CONTOURS IN FATHOMS
SURFACE SEDIMENTS
LAGUNA MADRE, TEXAS
AREA USUALLY EXPOSED
BAFFIN BAY
PADRE ISLAND
10
10
100
100
CLAY
CL.
S,CL.
ST,CL.
CL,S
S,S,C.
CL,ST
S.
ST, S.
S,ST.
ST.
SAND
SILT
N
PORT ISABEL
RIO
GRANDE
MEXICO
MEXICO

Fig. 4. Sediment distribution in Laguna Madre based on sand-silt-clay content.

northern Laguna Madre consists of a shelly sand. Oyster reefs on the other hand are very scarce and hence do not contribute much to the sediment. However, extensive reef growths of serpulid worms have effectively closed off most of the mouth of Baffin Bay. These worms are not known to be active at present.

The study of the sand-sized material under the microscope has shown that in much of the Laguna Madre the sand includes numerous finely crystalline calcareous and gypsum aggregates, which are virtually missing in San Antonio Bay. They are found, however, in some of the shallow evaporating ponds and marshes along the northern fringe of the barrier islands in the subhumid area. In addition to these calcareous aggregates, the sand grains often have a coating of calcium carbonate which develops into ooliths. These ooliths seem to form especially along the shores of the landward side of the northern

Laguna. Both the ooliths and the calcareous aggregates are aragonitic and are an indication of the aridity of the climate and the resulting high evaporation which causes precipitation of calcium carbonate.

Foraminifera appear to be somewhat less abundant in the Laguna Madre sediments than in those of the bays to the north. Furthermore, the Foraminifera assemblage contains a larger percentage of the Miliolidae than is found in the humid bays. These Miliolidae also are important in the shallow water around the bay fringes of the barrier islands in the humid areas (Parker, *et al.*, 1953).

One large contrast between the bay deposits of this area of Laguna Madre and those to the north is the rather extensive development of stratification in the Laguna deposits. The greater part of the cores obtained to date show this stratification. Apparently the burrowing organisms which stir the bottom so extensively in the northern Texas bays are not nearly as active in the Laguna. This may be partly because of the hypersaline conditions found in the Laguna and the local development of black stinking muds which are inhospitable to the boring organisms. In the buried sediments of the Laguna rosettes of gypsum develop locally. These seem to develop in a zone several feet below the surface (Masson, 1955). The rosettes are found in some abundance on the spoil banks which have been built above the surface by the dredging operations of the intercoastal canal. In places where the water is either very shallow or where the surface is intermittently covered, an algal mat has formed on the surface of the sediments.

On the other hand, the Laguna Madre sediments do have some characteristics in common with those of the northern bays. Thus they lack echinoids and glauconite and the quartzose sand content varies directly with the distance from the barrier island, as is also the case in most of the northern bays.

Incidental Sediment Types in the Northern Bays

In addition to the types of sediment already discussed for the subhumid area, there are some rather special conditions which need to be considered. In an extensive portion of Aransas Bay the nature of the sediments indicates that they are accumulating very slowly. The map (Fig. 2) shows that this portion of Aransas Bay lies at a considerable distance from any stream mouth and it is far enough inside the bay to be away from much influence from Aransas Pass. Furthermore, the adjacent barrier island does not have many migrating dunes or excess supply of sand. Also, the relatively deep water, much of it over 12 feet, prevents the waves from introducing large quantities of sediments from the shallow margins. As a result of the slow sediment accumulation, the benthonic Foraminifera constitute an appreciable fraction, while quartzose sand percentage is diminished. This is particularly well shown in the ½–¼ mm. and ¼–⅛ mm. sievings from these bay sediments. These fractions commonly contain more than 80 per cent Foraminifera. This condition of slow deposition with high Foraminifera percentages is found also in a few samples from lower San Antonio Bay, but is better represented in some of the San Antonio Bay borings a short distance below the sediment surface. The increase in the Foraminifera content at depth has been used as evidence that the rate of deposition was slower in a period shortly preceding the present (Moore, 1955). A search for other localities with this high percentage of Foraminifera has not been very successful, although one zone was discovered in a sample presented to us by the Texas A. & M. Research Foundation from central Matagorda Bay, where again the water is relatively deep.

A few samples taken from the bays along the northeastern margin of Texas and into western Louisiana suggested that a special characteristic of the sediment may exist in these places. Much higher than normal wood fiber or plant fiber content was found in the sediments of some of these bays. Peaty material and tree remains form a significant portion of this sediment.

Summary and Conclusions

Texas bay deposits have such definite environmental characteristics that these bay facies should be easily recognized in the Tertiary sediments which are now largely buried by the Recent deposits along the Texas coast. In the older formations the finding of extensive thicknesses of unstratified clayey sediments, with occasional intercalation of calcareous deposits, consisting dominantly of oyster shells, should indicate that bay conditions in a relatively humid area have existed. The absence of echinoids and glauconite in the coarser fractions of the sediment would help to confirm the lagoonal or estuarine origin of such deposits. The macroorganisms, the Foraminifera, and the Ostracoda all have assemblages which are characteristic of bays, and they are quite distinct from those found in the open Gulf (see Parker *et al.*, 1953, Swain, 1955, and Parker, 1955). Where the sediments are intercalated with large quantities of sand, the nearness to inlets or to barrier islands is suggested. Where the sediments are predominantly clay and where they have an abundance of wood fragments the nearness to a stream mouth is indicated. Also an occasional finding of silt and clay laminations suggests conditions of deposition at a stream mouth.

Finding of roughly stratified sediments high in sand content and containing gypsum and carbonate aggregates would indicate deposition of the sediments under conditions of excessive evaporation. The abundance of the calcareous ooliths and of calcareous coatings around shells and sand grains would also indicate these semi-arid bay conditions.

REFERENCES

Beal, M. A., and F. P. Shepard. 1956. A use of roundness to determine depositional environments. Jour. Sed. Pet., 26: 49–60.

Bullard, F. M. 1942. Source of beach and river sands on Gulf Coast of Texas. Bull. Geol. Soc. Amer., 53: 1021–1044.

Flint, R. F. 1953. Probable Wisconsin substages and Late-Wisconsin events in northeastern United States and southeastern Canada. Bull. Geol. Soc. Amer., 64: 912.

Grim, R. E., and W. D. Johns. 1955. Clay mineral investigation of sediments in the northern Gulf of Mexico. 2nd Nat'l. Conf. on Clays and Clay Minerals, Nat'l Research Council, 81–103.

Inman, D. L., and T. K. Chamberlain. 1955. Particle-size distribution in nearshore sediments. Soc. of Econ. Paleon. Miner. Spec. Publ. No. 3, 106–127.

Ladd, H. S. 1951. Brackish-water and marine assemblages of the Texas coast, with special reference to mollusks. Pub. Inst. Mar. Sci. Univ. Texas, 2: 125–164.

Lohse, E. A. 1955. Dynamic geology of the Modern Coastal Region, Northwest Gulf of Mexico. Soc. Econ. Paleon. Miner., Spec. Pub., 3: 99–105.

Masson, P. H. 1955. An occurrence of gypsum in southwest Texas. J. Sediment. Petrol., 25: 72–77.

Moore, D. G. 1955. Rate of deposition shown by relative abundance of Foraminifera. Bull. Amer. Assoc. Petrol. Geol., 39: 1594–1600.

Norris, R. M. 1953. Buried oyster reefs in some Texas bays. J. Paleont., 27: 569–76.

Parker, Frances L., F. B. Phleger, and J. F. Pierson. 1953. Ecology of Foraminifera from San Antonio Bay and environs, southwest Texas. Cushman Foundation Spec. Pub., 2: 1–75.

Parker, R. H. 1955. Changes in the invertebrate fauna, apparently attributable to salinity changes, in the bays of central Texas. J. Paleont., 29: 193–211.

Puffer, E. L., and W. K. Emerson. 1953. The molluscan community of the oyster-reef biotope on the central Texas coast. J. Paleont., 27: 537–544.

Shepard, F. P. 1953. Sedimentation rates in Texas estuaries and lagoons. Bull. Amer. Assoc. Petrol. Geol., 37: 1919–1934.

————. 1955. Stratigraphic research that may pay off. Oil and Gas Journal, Feb. 21, 4 pp.

————. 1956. Late Pleistocene and recent history of the central Texas coast. J. Geol., 64: 56–69.

Shepard, F. P., and D. G. Moore. 1955. Central Texas coast sedimentation: characteristics of sedimentary environment, recent history, and diagenesis. Bull. Amer. Assoc. Petrol. Geol., 39: 1463–1593.

————. 1953. Sediment zones bordering the barrier islands of central Texas coast. Soc. Econ. Paleon. Miner. Spec. Publ. No. 3: 78–96.

Swain, F. M. 1955. Ostracoda of San Antonio Bay, Texas. J. Paleont., 29: 561–646.

Thornthwaite, C. W. 1948. An approach toward a rational classification of climate. Geogr. Rev., 38: 55–94.

A Method for Measuring Eddy Diffusion in Coastal Embayments[1]

FRANK W. MOON, JR., CHARLES L. BRETSCHNEIDER
AND DONALD W. HOOD

Foreword

The primary purpose of this work was to devise a method of measuring the mixing of relatively small water masses in bays, estuaries and lagoons and to measure currents of slow velocity. Conventional mechanical current meters cannot be used to measure very slow currents. The method described consists of introducing a fluorescent dye into water at some point of interest and taking measurements along its path. By means of suitable instrumentation, transverse cross sections of the fluorescein concentration can be made at points downstream, from which the flow characteristics can be determined. This paper contains a description of the instrument used for the detection of trace quantities of fluorescein in water masses. Data obtained during a preliminary operation run have been analyzed and are included.

Methods of measuring the eddy diffusivity existing in fresh marine and oceanic basins of the world have been under investigation for several years. The problem is of major importance in consideration of processes which occur in aquatic media. The rate of mixing of nutrients, metabolites, or anti-metabolites; transfer processes across interfaces; effects of municipal and industrial outfalls; and rate of establishment of homogeneity across gradients can only be determined after a complete knowledge of the mixing processes involved is obtained.

The results of a number of diffusion studies have been reported in the literature. Stommel (1947) has treated the topic theoretically. Munk, Ewing, and Revelle (1949) investigated diffusion in the Bikini Lagoon. Ketchum and Ford (1952) studied the rate of dispersion in the wake of a barge at sea. Some data have also been provided by McLean (1952) who used fluorescein dye for tracing pollution in drinking water and Sturm and Johnson (1950) who used chemical tracers in following flood water. In 1955 Seligman (1955) reported results obtained by the use of fluorescein in estimating diffusion in the Irish Sea. In these studies a number of methods have evolved.

Ketchum (1951) in 1951 developed a method for determining the mixing of fresh and salt water applicable to certain types of estuaries in which fresh water was used as the indicator. This method is very general and mixing can be calculated from data at hand, but it gives no information regarding the currents involved, and the method is limited in that it can be used only in estuaries which are headed by rivers. In bays where very

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[1] Contribution from the Department of Oceanography of the Agricultural and Mechanical College of Texas, Oceanography and Meteorology Series No. 84; based in part on investigations conducted for the Texas A. & M. Research Foundation through sponsorship of Reynolds Metals Company and the Office of Naval Research through Contract No. N7onr-48702.

little fresh water enters, such as along the Texas coast, the above method fails. If horizontal diffusion is to be known under these conditions, an experiment must be conducted which will allow mixing to be observed.

In the work of Ketchum and Ford in studying the diffusion behind a barge at sea the ferrous ion was used as an indicator. In these experiments the peak concentration in the wake was difficult to determine because only discrete samples were obtained. Continuous transverse cross sections at a number of stations are needed. Not only does this allow for positive identification of the maximum concentration at the various stations in question, but it also gives the shape of the cross section of dispersion in the horizontal plane.

In seeking a suitable traceable substance the main objective is to obtain a water soluble substance which can be easily detected (preferably by a continuous system), be inexpensive, stable in sea water, and harmless in high concentrations. After investigating possible indicators, the sodium salt of fluorescein seemed to offer the greatest possibilities. There is some evidence (Seligman, 1955) that fluorescein deteriorates in sunlight but the rate is such that it appears applicable for short term studies.

Fluorescein can be easily detected by use of its fluorescent properties. Commercial instruments are available for fluorescence measurements in the laboratory, but these do not lend themselves to continuous shipboard operation. In the study discussed here an instrument which is described elsewhere (Moon, 1956) was constructed for this purpose. In this paper emphasis is placed on reporting and evaluating data obtained during a study of the diffusion processes occurring in Lydia Ann Channel near the Institute of Marine Sciences Laboratory at Port Aransas, Texas.

EXPERIMENTAL

Fluorescent Meter: The instrument consists of a high energy ultra-violet light source which is fed to a low fluorescent glass absorption cell through which the water being sampled is pumped. Corning glass filters are provided which pass non-dispersive fluorescent light to a photomultiplier tube. The tube current is then amplified and fed to a Esterline-Angus recorder. The instrument is capable of detecting somewhat less than 10^{-6} grams in one kilogram of sea water. By a system of range resistors, concentrations as great as 1×10^{-3} gms/liter may also be determined.

Calibration of Instrument: The instrument was standardized against sea water solutions containing gradient amounts of fluorescein dye. A standardization curve for known concentrations of fluorescein dye dissolved in sea water from the Lydia Ann Channel is shown in Figure 1.

Sampling System: A flexible rotor pump driven by an electric motor is used to circulate bay water through an aspirator which has its low pressure side connected to the exit side of the fluoresence cell. The inlet side of the cell is connected to the inlet hose, which is kept as short as possible and has as small a diameter as practical.

The circulation of water through the aspirator creates a low pressure in the sampling system which causes bay water to flow through the inlet hose into the examination cell, then overboard with the effluent of the circulation pump.

The response time of the instrument is largely determined by the rate of flow and the volume of water in the sampling system between the end of the inlet hose and the examination cell. The upper limit of flow is reached when an air pocket appears in the fluorescence cell.

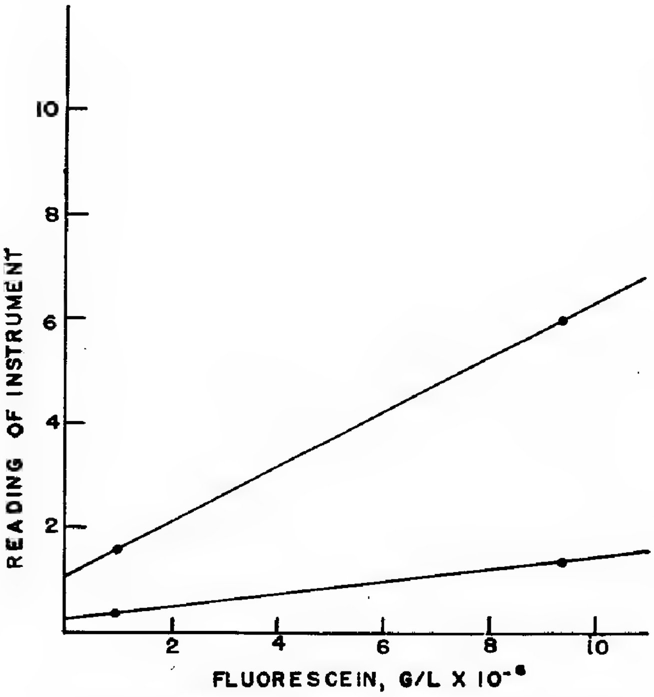

Fig. 1. Standard curve for sodium salt of fluorescein concentration vs. meter reading. Bottom line range five; top line range six; seven ranges are available.

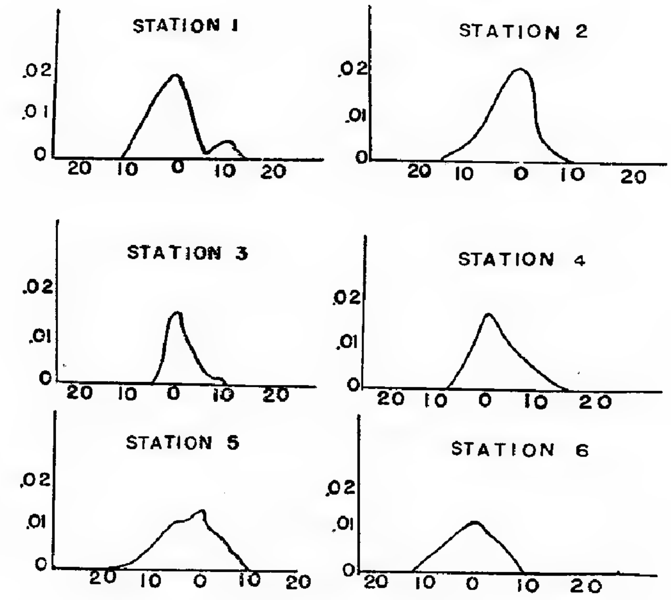

Fig. 3. Log of concentration of fluorescein plotted against distance from the point of introduction. The ordinate is the concentration of fluorescein in PPM; the abscissa is distance in feet.

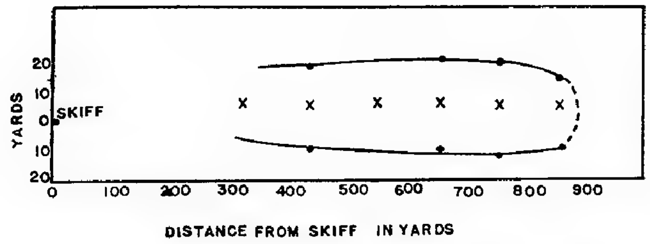

Fig. 2. Envelope of fluorescein and station locations.
X—Location of maximum concentration.
•—Points of extinction of fluorescein.

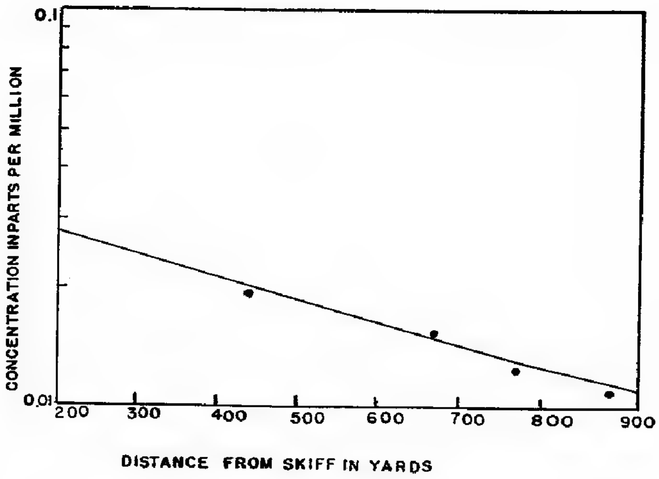

Fig. 4. Diffusion of fluorescein with distance showing the exponential pattern developed.

Labeling System: Components of the introduction system are located aboard a skiff which is anchored at a point of interest in the bay. A flexible rotor pump driven by gasoline engine circulates bay water from any desired depth through an aspirator, the low pressure side of which is connected to a reservoir. The reservoir contains an almost saturated solution of fluorescein in bay water. The inlet and outlet of this system are at the same level. Since the thermal structure of the circulated water is altered only slightly by the addition of the fluorescein, the treated water tends to remain with the original water mass.

Stability of fluorescein in water—Fluorescein is known to decay on exposure to sunlight over extended periods of time. When stored in the dark fluorescein dissolved in sea water has been found to continue to fluoresce under ultra-violet irradiation without changed intensity for periods up to one month. The duration of diffusion experiments seldom extends beyond a few hours and errors introduced because of the loss of the fluorescent properties of the tracer during short periods is thought to be within the experimental error of the method.

Concentration of fluorescein used in labeling—The sodium salt of fluorescein has a solubility in sea water of about 100 gms/kilogram. However, it was found that a concentration of 450 grams in five gallons of water (2,400 ppm) was satisfactory for supplying the aspirator of the introduction system.

Field Work: A successful experiment was conducted on November 20, 1954. The study was made in the Lydia Ann Channel between the abandoned lighthouse and a point about one mile north in the channel.

The skiff was anchored at the west edge of the channel in twelve feet of water. The fluorescein was dispersed into the channel at a depth of six feet. All sampling in this experiment was also done at the six-foot level. The fluorescein was mixed in the aspirator arrangement with water also taken from the six-foot level.

Steady state conditions were established after about 60 minutes of time had elapsed. Six crossings of the plume were found to yield useful data. The nature of the plume and the location of the center at each crossing is indicated in Figure 2. A buoy was dropped at the center of each plume on crossing. The location of this buoy was then later established by obtaining fixes on charted landmarks.

At the six-foot level a current of 0.29 knots was measured from the skiff at 2:27 P.M. CST. At 3:42 a current of 0.33 knots was observed. These currents were measured with a Price current meter.

Presentation of Data: Concentrations of fluorescein at typical stations are presented in the cross sections shown in Figure 3. A plot of the peak concentrations against distance from the skiff is shown in Figure 4. The curve was found to depart from the straight line at distances less than 200 yards. This is to be expected since near the point of origin diffusion occurred in the vertical as well as in the horizontal plane. The diffusion became essentially horizontal past a point 200 yards from the origin.

THEORETICAL

The equation for the local rate of a concentration S at a position x, y, z at time t is governed by advection and diffusion according to the relation (Sverdrup *et al.*, 1942, p. 159).

$$\frac{\delta s}{\delta t} = \frac{\delta}{\delta x}\left[\frac{Ax}{\rho}\frac{\delta s}{\delta x}\right] + \frac{\delta}{\delta y}\left[\frac{Ay}{\rho}\frac{\delta s}{\delta y}\right] + \frac{\delta}{\delta z}\left[\frac{Az}{\rho}\frac{\delta s}{\delta z}\right] - \left[V_x\frac{\delta s}{\delta x} + V_y\frac{\delta s}{\delta y} + V_z\frac{\delta s}{\delta z}\right] \quad (1)$$

where A_x, A_y, A_z are the eddy diffusivity coefficients for mixing in the x, y, and z directions respectively, V_x, V_y, V_z are the velocity components in the x, y, z directions, and ρ is the density.

For a two dimensional system where $A_x = A_y = A$, (A/ρ) being assumed constant) the condition for stationary distribution of S reduces to

$$\frac{A}{\rho}\frac{\delta^2 s}{\delta x^2} + \frac{A}{\rho}\frac{\delta^2 s}{\delta y^2} = V_x\frac{\delta s}{\delta x} + V_y\frac{\delta s}{\delta y}$$

If the current is assumed along the x coordinate, diffusion in this direction can be neglected, V_y must be zero and the equation reduces to

$$\frac{A}{\rho}\frac{\delta^2 s}{\delta y^2} = V_x \frac{\delta s}{\delta x} \tag{2}$$

where A = eddy diffusivity in gm./cm.–sec.
V_x = velocity in the x direction in cm./sec.
ρ = density in gm./ml.
S = concentration of matter in parts per million (PPM).

Let

$$\frac{A}{\rho Vx} = \alpha^2$$

then (2) becomes

$$\frac{\delta s}{\delta x} = \alpha^2 \frac{\delta^2 s}{\delta y^2} \tag{3}$$

The outline for a general solution of this partial differential equation can be found in reference (Sokolnikoff *et al.*, 1941, p. 373).

By choosing the boundary condition to be satisfied at x = 0, as

$$S = S_o \text{ (SC) } \frac{\pi}{2L} y \text{ for } (-L \leq y \leq L)$$

the assumption is made that, at each cross section, the shape of the distribution curve can be approximated by a simple cosine function. The constant, L, is the maximum half width, the distance in the y direction beyond which no fluorescein can be detected.

Let s be some function of x and y, for instance

$$S = X(x)Y(y)$$

Then by substitution in (3)

$$\frac{1}{\alpha^2 X}\frac{dX}{dx} = \frac{1}{y}\frac{d^2Y}{dy^2} \tag{4}$$

This equation can hold only if each member is equal to some constant, say—β^2, such that

$$\frac{1}{\alpha^2 X}\frac{dX}{dx} = \frac{1}{Y}\frac{d^2Y}{dy^2} = -\beta^2 \tag{5}$$

It can be seen that

$$\frac{dX}{dx} + \alpha^2\beta^2 X = 0 \tag{6}$$

and

$$\frac{d^2Y}{dy^2} + \beta^2 Y = 0 \tag{7}$$

Equations (6) and (7) are ordinary, homogeneous, differential equations.
Two particular solutions possible are

$$X = e^{-\alpha^2\beta^2 x} \qquad Y = K\cos\beta y$$

By substitution in (4)

$$S = Ke^{-\alpha^2\beta x} \quad \cos\beta y$$

Applying the boundary conditions

$$S = K\cos\beta\, y = S_o \cos\frac{\pi}{2L}\, y$$

By choosing $K = S_o$ and $\rho = \frac{\pi}{2L}$, the boundary condition is satisfied. Restricting consideration to points of maximum concentration ($y = 0$),
the solution becomes

$$S = S_o e^{-\left(\frac{A}{\rho V x}\right)\left(\frac{\pi}{2L}\right)^2 X}$$

CALCULATIONS

The equation

$$S = S_o e^{-\alpha^2\beta^2 x}$$

is used in these calculations. If X is allowed to be 0 at 39,200 cm (430 yards) from the skiff then X is zero, S is S_o and the concentration of fluorescein is 0.0195 PPM. Two crossings were chosen for this calculation. These were at 60,400 cm (660 yards) and 69,500 cm (760) yards. The temperature was 20°C; salinity 36.58‰; density was 1.026 gms/cm and the velocity V_x was 15.4 cm/sec.

	60,400 cm	69,500 cm
$X =$	21,200 cm	= 30,300 cm
$2L =$	2,020	= 3,130
$\beta^2 =$	2.4×10^{-6}	$= 1 \times 10^{-6}$
$S =$	0.0155 PPM	= 0.0125 PPM
$\alpha^2 =$	4.52	= 14.9
$A =$	71.4	= 236

Stommel has reported values of neighbor diffusivity from data taken at Blairmore, Woods Hole and Bermuda (1947). By using the relation $F(l) = 3.03\,K$ (where $F(l)$ = neighbor diffusivity, $K = A/\rho$ eddy diffusivity) it is possible to compare this author's values with the ones obtained here. These values are 211 and 697 for 60,400 and 69,500 cm, respectively.

Figure 4 is taken from Figure 2, reference (Stommel, 1947). Results of the calculations presented here are included for comparison with the values obtained by Stommel. It is not inferred that this work in any way tends to prove, or disprove, the 4/3 law postulated by Richardson and Stommel in their respective articles (1939) and (1947). However, it does show the interesting fact that the values of diffusion obtained by using the fluorescence meter method are comparable to values reported elsewhere.

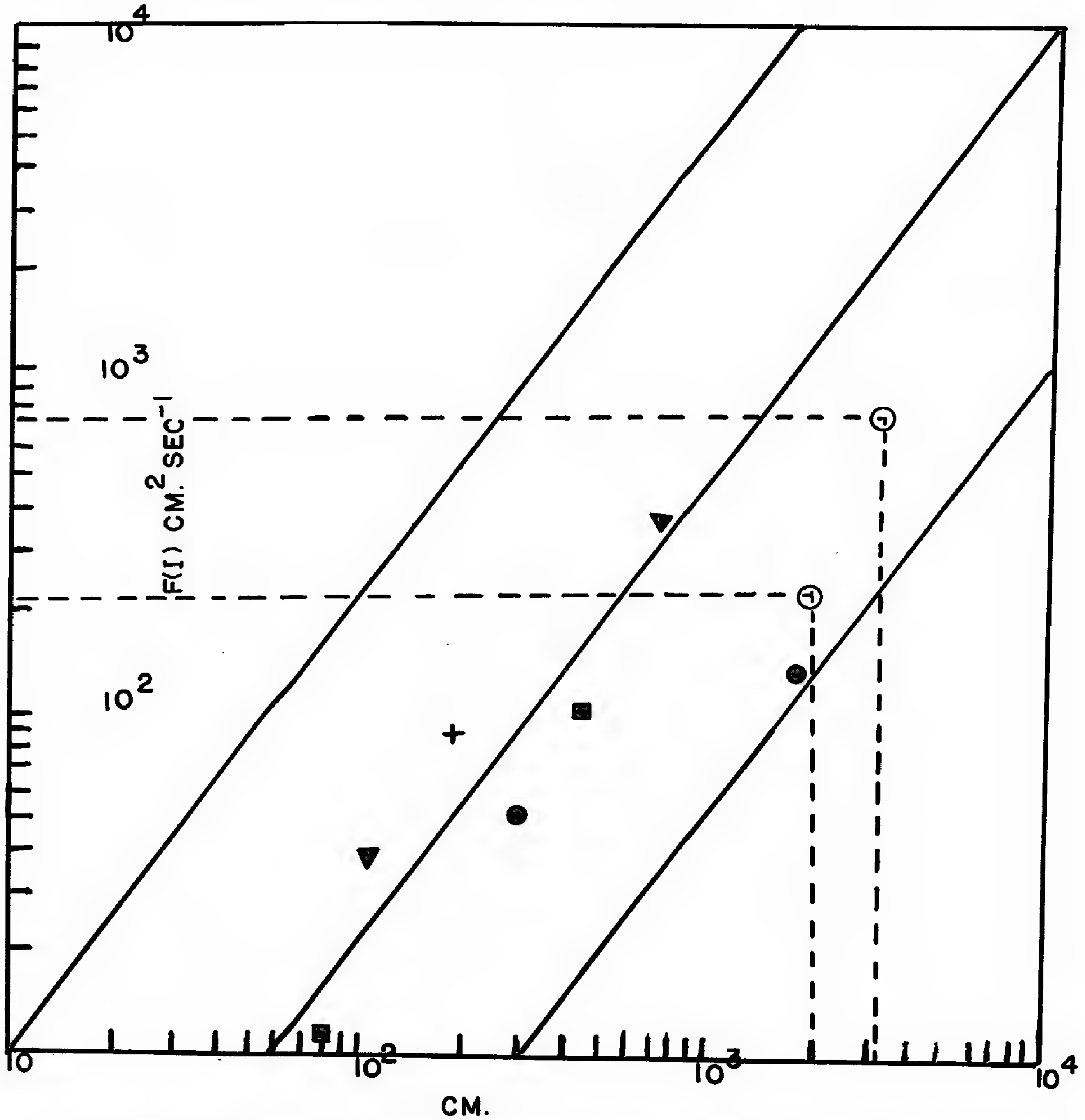

Fig. 5. Neighbor Diffusivity vs. Neighbor Separation Data from Stommel (1947). Dotted line indicates data from this paper.

CONCLUSIONS

The method of determining rates of diffusion described in this paper has many advantages to others reported in the literature. The marking substance, fluorescein, can be introduced into the water mass conveniently and can be identified in concentrations low enough to keep material costs at a minimum. The low levels of fluorescence occurring in the environment can easily be compensated and other sources of fluorescence are not likely.

Further, a sensing instrument may be used for a continuous sampling rather than discrete sampling. A permanent record is made in the field which can be examined,

It is believed that this method of determining diffusion will prove to be of value in problems concerning waste and sewage disposal and in other studies where an accurate evaluation of diffusion is required.

immediately or later at a shore station or laboratory.

LITERATURE CITED

Burdett, R. A. and L. C. Jones. 1947. The Photoelectric Measurement of Flourescent Spectra. J. Opt. Soc. Amer. 37: 554–557.

Cram, W. S. 1936. Einfluss der Temperatur dur Uraninlösung auf die Abklingzeit dur Fluoresxenz. Z. für Physik, 103: 551–559.

Dake, H. C. and Jack DeMent. 1941. Fluorescent Light and Its Applications. Chemical Publishing Co., Brooklyn, N. Y., 192 pp.

DeMent, Jack. 1945. Fluorochemistry. Chemical Publishing Co., Brooklyn, N. Y., 242 pp.

Ketchum, B. H. 1951. The Exchange of Fresh and Salt Water in Tidal Estuaries, J. Mar. Res., 10: 18–38.

Ketchum, B. H. and W. L. Ford. 1952. Rate of Dispersion in the Wake of a Barge at Sea. Trans. Amer. Geophys. Un., 33: 680–684.

Lowry, O. H. 1948. A Microphoto Fluorometer. J. of Biol. Chem., 173: 677–682.

McLean, Ruth A. 1952. Fluorescence of Drinking Water as Evidence of Sewage Pollution. J. Amer. Water Wks. Assn., 38: 355–360.

Moon, F. W., Jr. 1953. A Continuous Reading Fluorescence Meter for Eddy Diffusion Studies. Unpublished Thesis, A. & M. College of Texas.

Munk, W. H., G. C. Ewing and R. R. Revelle. 1949. Diffusion in Bikini Lagoon. Trans. Geophys. Un., 30: 59–66.

Pritchard, D. W. and W. V. Burt. 1951. An Inexpensive and Rapid Technique for Obtaining Current Profiles in Estuarine Waters. J. Mar. Res., 10: 180–189.

R. C. A. Phototubes. 1950. Cathode-ray and Special Tubes Booklet, Form No. CRPS–102a.

R. C. A. Receiving Tube Manual. 1950. Technical Series RC 16.

Reed, D. G. and T. Stewart. 1949. A Streamline Cable Depressor. J. Mar. Res., 8: 226–236.

Richardson, L. F. 1939. Atmospheric Diffusion Shown on a Distance-Neighbor Graph. Proc. Roy. Soc., Ser. A, 110: 709–727.

Richter, Walther. 1947. Fundamentals of Industrial Electronic Circuits. McGraw Hill, New York, N. Y., pp. 486–487 and 218–223.

Seligman, Henry. 1955. International Conference on the Peaceful Uses of Atomic Energy. Paper No. 419.

Sverdrup, H. U., M. W. Johnson and R. H. Fleming. 1942. The Oceans. Prentice-Hall, New York, N. Y.

Sokolnikoff, I. S. and E. S. Sokolnikoff. 1941. Higher Mathematics for Engineers and Physicists. McGraw-Hill, New York, N. Y.

Stommel, Henry. 1947. Horizontal Diffusion Due to Oceanic Turbulence. J. Mar. Res. 8: 199–225.

Sturm, P. W. and W. E. Johnson. 1950. Field Experiments with Chemical Tracers in Flood Waters. Producers Monthly, 15 (no. 2): 11–17.

Strontium in Natural Waters

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Introduction

HISTORICAL SKETCH

Not long after the discovery of strontium in 1790, search for the element in nature revealed a widespread distribution of the element in waters. During the early nineteenth century many qualitative and a few quantitative determinations were made indicating considerable quantities of strontium in mineral springs and brines (Mellor, 1923). Forchhammer in 1865 and Dieulafait in 1877 discovered much strontium in the ocean also, which subsequently led to a series of varying estimates for the strontium content of normal sea water of salinity 35 parts per thousand.

Desgrez and Meunier (1926) found 8.7 mg/l with arc spectrograph of sulfate precipitate; Thomas and Thompson (Thompson and Robinson, 1932) found 13.2 mg/l; Ramage (1936) reported 40–50 mg/l with a flame method; Noll (1934) found 7.0–7.8 mg/l with x-ray spectral methods on oxalate precipitates; Miyake (1939) found 14.4 mg/l gravimetrically after separation with nitrate; Vinogradov found 8.0 and

10.0 mg/l (Vinogradov, 1938; Vinogradov and Borovik-Romanova, 1945). Then at about the same time several new studies fixed the value for the ocean within a small range of uncertainty. Smales (1951) found 10.0 mg/l with flame and radioactive methods; Chow and Thompson (1955) found 8.0 mg/l with flame methods directly on sea water; Bowen (1956) found 8.5 mg/l by neutron activation; Hummel and Smales (1956) found 8.0 mg/l with radioactive and stable isotopes; and Odum (1950b, 1951b) reported 8.1 mg/l with flame methods on oxalate precipitates. Thus it seems agreed that the Sr/Ca ratio of sea water is close to 8 mg/l (Sr/Ca Ratio, 9.0 atoms/1000 atoms).

Reliable modern analyses of fresh waters have been few. Lohammar (1938) reported a series for Swedish lakes, Odum (1951c) reported data from Florida, Wilska (1952) from Finland, and Borovik-Romanova, Korolev and Kutsenko (1954) from Russia. Further analyses were reported by Straub (1950) and McGrain and Thomas (1951).

In saline waters some uncertain and fragmentary data on water residues are reported by Clarke (1924). Francis (1923) observed some high strontium values in natural brines which he interpreted as due to the increased solubility of saline water. Delecourt (1946) interpreted some analyses of high strontium in ground brine by Camaran (1946) as an indication of little changed ancient ocean water with a hypothesis that strontium had decreased in recent geological ages. This is doubtful since the Sr/Ca ratio of this brine 4.6/1000 by atoms was actually lower than that for the present sea (9.23/1000).

Increased interest related to atomic energy due to the difficulties in dealing with strontium 90, a long lived by-product of fission led to new studies. Alexander, Nusbaum, and MacDonald (1954) analyzed surface waters and ground waters relative to 50 municipal water supplies in the United States. The widespread coverage of these data help permit generalizations regarding the geochemical distribution of strontium in waters.

If the trace element contents of fossils and rocks are to be used to indicate something of the nature of aquatic depositional environments paleoecologically, the relationship of the strontium/calcium ratio to regional water types must be understood. This was one motivation which led to further analysis.

METHODS

New analyses of waters in this paper were made with a flame photometric determination on calcium and strontium chloride solutions. These solutions were prepared from evaporates of 4 liter samples of fresh water as follows. After ashing and extracting with hydrochloric acid, ammonium oxalate 5 to 10 times in excess was added to the acid solutions which were then adjusted slowly at boiling temperatures to basic conditions with ammonium hydroxide. The resulting oxalate precipitates of calcium and strontium were collected on filter paper, ashed at 600 deg. to carbonates and redissolved in 20% HCl at approximately 0.1 M Calcium.

The intensity of the flame emission at 4607A for strontium and 4227A for calcium was estimated from flame in which moist air was passed through a nebulizer and into the air intake of a Fisher burner lined with a glass inner jacket. A flame photometer was devised from a qualitative, classroom, Cenco grating spectrograph by mounting a photomultiplier tube opposite the calcium line and another opposite the strontium line. The output of the photomultiplier tubes was passed into a D. C. amplifier and read on a 10 inch, zero to 50, microameter. With this apparatus it was possible to read strontium, calcium, and the background blue flame successively in a few seconds by tilting the nebulizer and by throwing a circuit switch to indicate first the calcium emission and then the strontium emission. Standards were made from known carbonate concentrations also dissolved in 20% HCl. Laborious as these methods are, they have insured that all interference of foreign substances was eliminated.

In the course of development of these techniques, it was found that direct flame analysis of extracts of evaporate residues was not feasible as indicated by Table 1 where analyses before oxalate separation were widely in error. The strontium values reported by Braidech and Emery (1935) in an arc spectrographic study of a number of elements in evaporates were simmilarly erratic and about 10 times too high presumably because of interference of other ions.

TABLE 1

Distortion of Analyses of Lake Waters Because of Different Composition of Standards and Evaporates

Evaporates		Oxalate Precipitate		Rough Gravimetric
Sr/Ca atoms/1000 atoms	Spectrographic calcium mg/l	Sr/Ca atoms/1000 atoms	Spectrographic calcium mg/l	Calcium mg/l
0.25	10.5	1.32	21.4	23.6
1.92	11.6	1.32	31.8	......
1.30	14.3	0.91	20.7	23.7
2.82	17.6	1.32	28.7	32.2
3.73	14.3	1.08	28.4	28.4
24.6	1.47	1.67	5.5	5.4
32.8	5.2	2.88	1.2	2.1
10.7	5.4	2.05	11.4	13.3
5.84	1.24	1.27	6.8	7.4
37.7	8.3	2.44	2.8	4.0
5.3	0.41	1.44	2.9	3.1

Sea water analyses were made with ammonium oxalate precipitations from 100 cc samples processed similarly. As indicated in Table 2 occlusion of sodium occurred in two series which also registered slightly higher strontium values. It was presumed that these values were too high due to stray light from sodium emission. The values for double precipitations were presumed to be too small because of some strontium loss in the extra precipitation.

ACKNOWLEDGMENTS

Data are from a Ph.D. dissertation, The Biogeochemistry of Strontium, 1950, Yale University with additional analyses made in 1952 in the Biology department, University of Florida, Gainesville, Florida. The inspirational direction of George Evelyn Hutchinson is gratefully acknowledged. Thanks are expressed to R. Hellman, Claude Adams, Willard Hartman, M. Passano, B. Ross Livingston, and R. Benoit for collection of samples. A. D. Hasler made available the residues from Wisconsin and Philippine lakes.

More Data on Strontium in Waters

The new data are presented in Table 3 in a classification into springs, rivers and streams, lake regions, and closed basins. Included are some published data of others

TABLE 2

Strontium Analyses of Sea Water

Location, Method	Number of Analyses	Sr/Ca Atoms Per 1000 Atoms	
		Mean	Range
LONG ISLAND SOUND, 1943–48, Salinity, 28–33 ‰;			
Temp., 0.0–20° C.; top and bottom samples:			
Arc spectrograph, log sector, oxalate precipitates, 1948	12	8.8	6.8 –12.3
Flame spectrophotometer, oxalate precipitates, some occluded sodium; concentration of solutions, 0.1 molar calcium; two analyses from each sample bottle, 1949*	120	9.21	6.72–12.0
Flame spectrophotometer, oxalate separations twice precipitated, concentration of solutions 0.1 molar calcium	16	8.72	7.91–10.00
Flame spectrophotometer, oxalate separations varied precipitation procedures; 0.1 molar calcium solutions*	12	8.90	8.32–10.00
Flame spectrophotometer, carbonate precipitations, 0.1 molar calcium solutions	5	11.34	4.9 –13.3
ATLANTIC OCEAN STATIONS			
30° 54′ N Lat., 62° 10′ W Long., Dec. 19, 1947; 31° 34′ N Lat., 36° 29′ W Long., Dec. 27, 1947; 35° 23′ N Lat., 10° 22′ W Long., Jan. 4, 1948; Off Hatteras, N. C., January, 1950; Depth, 1–4415 meters; Salinity, 34.9–36.9 ‰; Temperature, 0.02–22.3° C. Flame spectrophotometer, much occluded sodium, 1950			
Concentration of solutions, 0.2 molar calcium	47	10.96	10.22–11.08
Concentration of solutions, 0.05 molar calcium*	39	9.76	8.78–12.09
*Preferred value, mean of starred values, reported previously (Odum, 1951)		9.23	

for comparison as indicated. Because strontium is most nearly related to calcium among chemical elements it tends to be correlated in distribution. By expressing the data as Sr/Ca ratio by atoms some idea of the behavior of strontium relative to the better known calcium can be easily determined.

In Figure 1 are plotted representative data from Table 3 on coordinates of Sr/Ca ratio and approximate chlorinity. In Figure 2 coordinates of Sr/Ca and Ca are used. The relationship of strontium to some general classes of natural waters is indicated. These patterns can be explained in part by consideration of some aspects of the strontium cycle as described in the following paragraphs.

Whereas Rodhe (1951) found strontium in fresh waters of Sweden to bear a constant ratio to the conductivity and to the major ions, this relationship breaks down when waters from more diverse regions are compared (Figures 1 and 2).

Factors Controlling Strontium Content in Waters

THE EDAPHIC GEOCHEMICAL FACTOR

When acid rainwater falls and percolates soil and rock, it acquires strontium and calcium especially from those minerals and deposits which are both soluble and rich

TABLE 3

Strontium in Natural Waters

Name of Body of Water	Ca Milligrams Per Liter	Sr/Ca Atoms/1000 Atoms	Sr Micrograms Per Liter
FLORIDA SPRINGS			
Fanning Springs, Old Town, Levy Co., May 6, 1951	66.0	1.16	168
Blue Springs, Bronson, Levy Co., May 6, 1951	28.0	0.80	49
Troy Springs, Lafayette Co., May 6, 1951	54.7	0.79	95
Manatee Springs, Chiefland, Levy Co., May 6, 1951	31.7	2.50	173
Ichatucknee Springs, Columbia Co., May 13, 1951	50.3	1.25	137
Hart Springs, Wilcox, Gilchrist Co., May 13, 1951	66.7	0.85	124
Silver Springs, Marion Co., Nov. 25, 1950	71.6	5.0	784
Poe Springs, Alachua Co., Dec., 1950	63.7	3.0	418
Blue Springs, Gilchrist Co., Dec., 1950	53.3	1.78	208
Crystal Springs, Pasco Co., Dec., 1950	52.8	4.1	474
Orange Springs, Marion Co., Nov. 25, 1950	40.5	3.3	293
Chassahowitzka Springs, Citrus Co., Feb. 23, 1951	43.7	3.5	335
Mud Spring, Welaka, Putnam Co., March, 1951	44.4	8.0	778
Beecher Spring, Welaka, Putnam Co., March, 1951	42.6	5.7	485
Magnesia Springs, Alachua Co., Jan. 21, 1951	35.9	3.4	268
Rainbow Springs, Marion Co., Feb. 23, 1951	18.9	2.0	83
Juniper Springs, Marion Co., Nov. 25, 1950	13.7	4.9	147
Glenn Springs, Alachua Co., Jan. 15, 1950	14.6	1.35	43.2
Devils Mill Hopper, Alachua Co., April, 1950	24.4	2.0	107
Iron Spring, Hawthorne, Alachua Co., May, 1951	0.52	10	11
Salt Springs, Marion Co., Nov. 25, 1950	240	9.3, 12.3	4890
Silver Glen Springs, Marion Co., Nov. 25, 1950	87	7.9	687
Homossassa Springs, Citrus Co., Feb. 23, 1951	52.2	5.2	595
RIVERS AND STREAMS			
Housatonic River, Conn., Dec., 1949	22.9	0.91	45.6
Roundout Creek, Rosendale, N. Y., Dec., 1949	12.2	3.48	93.
Hudson River, Poughkeepsie, N. Y., Dec., 1949	18.6	2.65	107.9
James River, Richmond, Va., Feb. 17, 1950	10.5	1.80	41.4
Roanoke River, Henderson, N. C., Feb. 17, 1950	......	2.74	......
Delaware River, Newcastle Ferry, Feb., 1950	21.3	3.10	144
Withlacoochee River, Gulf Hammock, Fla., Feb. 23, 1951	43.2	3.7	350
St. Johns River, Welaka, Fla., March, 1951	38.5	8.1	683
Dunn Creek, St. Johns River, Welaka, Fla., March, 1951	36.4	10.5	837
Hogtown Creek, Gainesville, Fla., Jan., 1951	12.9	2.6	73.4
Prairie Creek, Gainesville, Fla., March, 1951	4.4	1.86	17.9
Appalachicola River, Chattahoochee, Fla., April, 1951	13.1	1.08	30.9
Suwanee River at Fanning Springs, Fla., April, 1951	28.6	1.80	111
Black Warrior River, Tuscaloose, Ala., April, 1951	5.1	1.76	19.1
Hatchet Creek, Gainesville, Fla., July, 1951	3.3	2.00	14.5
Boulder Creek, Colo. (Platte River) Clarke (1924)	6.7	4.2	61.5
Platte River, Colo. (Cache La Poudre) Clarke (1924)	31	3.8	258
LAKES			
Florida			
Sinks			
University of Florida (milk plant) Jan., 1951	34.6	2.20	167
Green sink (after rain) Aug. 29, 1951	12.6	1.18	33
Seepage lakes			
Newman's Lake, Gainesville, Jan. 21, 1951 Hawthorne, March, 1951	3.5	3.8	29
Lake Wauberg, Alachua Co., Jan., 1951	3.4	2.31	17
Hampton Lake, Bradford Co., June, 1951	1.7	3.22	12
High calcium lakes			
Lake Kanapaha, Gainesville, Jan., 1951	65.2	1.80	256
Fowler's Lake, Hawthorne, May, 1951	15.5	3.2	108
Bivin's Arm, Gainesville, Jan., 1951	37.6	2.10	173
Kentucky			
Devon Park Pond, Covington, Dec. 27, 1949	30.0	1.25	82
Wisconsin			
Trout Lake, June 27, 1925	8.8	2.31	44.4
Helmut Lake, Aug. 27, 1934	1.9	2.56	10.6
Helen Lake, Aug. 24, 1934	1.2	2.24	5.9

Lake Mary, Aug. 24, 1934	1.7	2.83	4.8
Lake Adelaide, Aug. 24, 1934	2.2	2.59	12.5
Nebish Lake, July 25, 1934	1.8	1.84	7.3
Lake Mendota, July 18, 1927	22.9	1.77	88.6
Lake Mendota (uncentrifuged)	20.2	2.10	92.7
Lake Mendota, July 25, 1928	25.3	1.16	64.2
Lake Erie, June 17, 1929	23.2	2.70	137.0
Maine			
Sabethday Lake, Cumberland Co., Dec., 1949	9.3	2.44	49.7
Sebago Lake, Cumberland Co., Dec., 1949	3.0	1.84	12.1
Range Pond, Androscoggin Co., Dec., 1949	3.0	1.47	9.7
Connecticut			
Low calcium lakes draining ancient crystalline rock			
Lake Quassapaug, Nov., 1949	2.1	2.88	13.2
Mt. Tom Pond, Nov., 1949	5.4	1.67	19.9
Westover School Pond, Nov., 1949	4.0	2.44	21.4
Beseck Lake, Nov., 1949	3.1	1.44	9.8
Monastery Pond, Nov., 1949	4.7	1.27	13.1
Lake Wintergreen Reservoir, Nov., 1949	4.0	2.50	21.9
Lake Waramaug, Nov., 1949	3.1	1.68	11.4
Bantam Lake, Nov., 1949	4.4	1.28	12.3
Seepage lakes			
Bethany Bog, May, 1950	1.9	2.01	8.5
Coldbrook Bog, Norfolk, May, Nov., 1949	1.6, 5.1	2.06	14.9
Moderate calcium lakes, more fertile, Triassic sediments			
Linsley Pond, Oct., 1949	13.3	2.05	59.6
Lake Quonnipaug, Nov., 1949	7.4	1.27	20.6
Clark Pond, Mill River, Nov. 25, 1949	15.8	1.31	45.3
Middletown Reservoir, Nov., 1949	14.2	2.46	76.5
Black Pond, Nov., 1949	11.3	1.73	42.8
Mt Carmel Pond, Nov. 25, 1949	10.0	0.86	18.8
Upper Linsley Pond, Dec. 15, 1949	......	1.92	......
Edgewood Park Pool, Nov., 1950	17.5	0.86	32.9
Wallingford Reservoir, Nov., 1950	20.1	2.02	88.8
Beardsley Pond, Conn., Nov., 1949	23.7	0.91	47.0
Bog Meadow Pond, Nov., 1949	28.4	1.08	67.0
Basalt drainage			
West Rock Park Pond (water film on mud) Dec. 1, 1949	21.9	2.10	100.7
High calcium lakes, limestone area			
Beeslick Pond, Nov., 1949	32.2	1.32	93.0
Lake Wononskopomac, Nov., 1949	23.6	1.32	68.2
East Twin Lake, Conn., Nov., 1949	31.8	1.32	91.9
North Carolina			
Piedmont, University Lake, Dec. 25, 1949	4.6	3.80	38.3
July, 1948	2.5, 3.2	5.90	32.2
Draining residual clays of ancient crystalline rocks			
Eastwood Lake, Orange Co., N. C., Dec. 25, 1949	3.8	3.57	29.7
Seepage lakes: Bladen Co., N. C.			
Jones Lakes, Dec. 24, 1949	0.32	4.30	3.0
Singletary Lake, Dec. 24, 1949	0.35	3.50	2.7
Lake Waccamaw (Miocene limestone outcrop) Dec. 24, 1949	6.3	2.39	33.0
Black Lake, Dec. 24, 1949	0.37	2.66	2.2
Sweden			
Average of 35 lakes (Lohammer, 1938)	20.60	1.35	......
Philippines			
Volcanic lakes			
Taal Lake, April 26, 1936	5.2	2.89	325.0
April 5, 1932	42.0	2.88	264.0
Laguna de Bay, March 16, 1932	8.7	4.72	89.7
Calibate Lake, March 4, 1932	68.4	5.00	750
April 3, 1932	......	5.00	......
CLOSED BASINS			
Ocean (see text)	400	9.23	8,100
Great Salt Lake, Utah (double precipitate) 1951	228	4.20	2,100
Utah Lake, data of Seidell (Clarke, 1924)	69	11.5	1,730

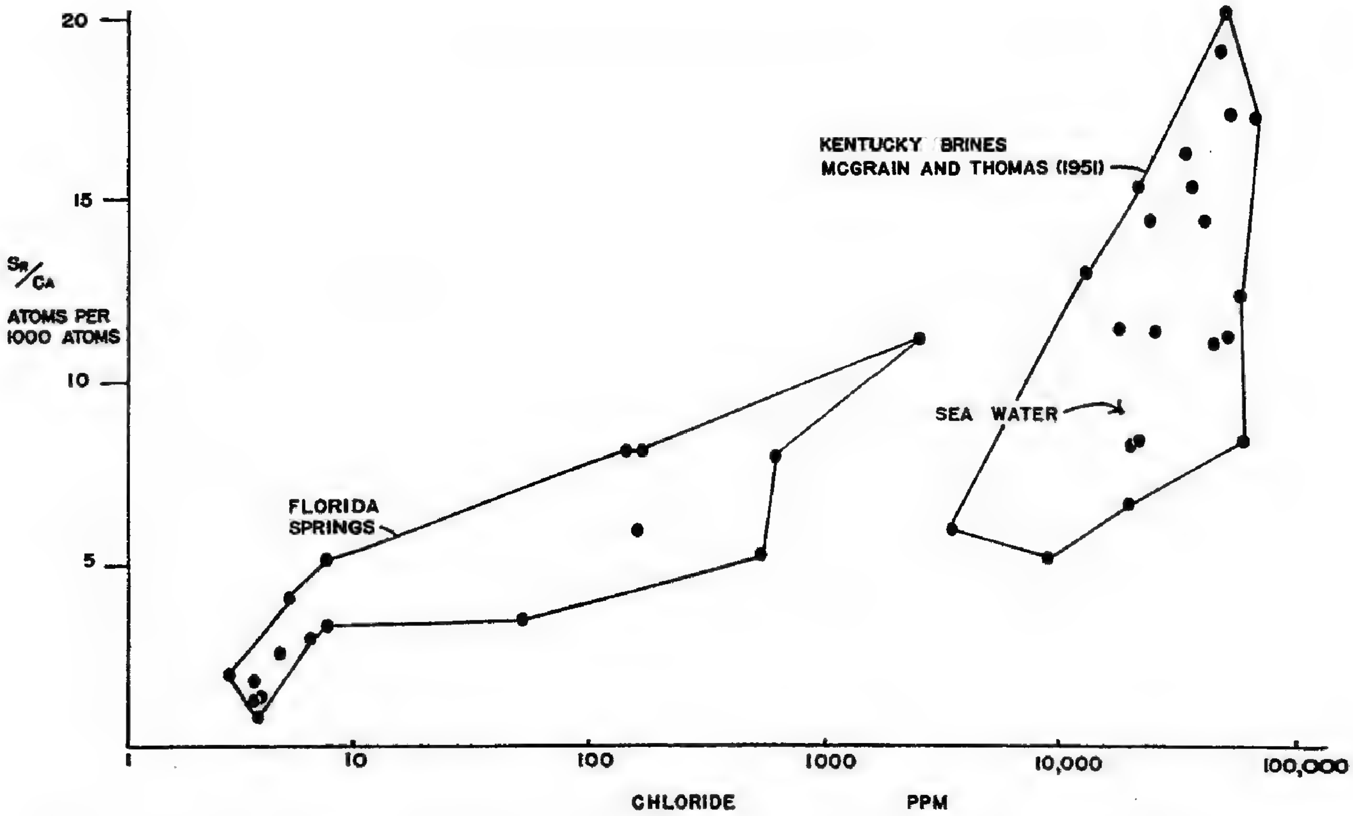

FIG. 1. Sr/Ca ratio of ground waters as a function of chlorinity in ppm. Data on Florida Springs are plotted as an example of a region with groundwaters at salinity less than sea water. Data on brines from Kentucky (McGrain and Thomas, 1951) are plotted representing ground waters with salinity greater than sea water. Several very high values of Sr/Ca ratio among the data on brines fall off the graph.

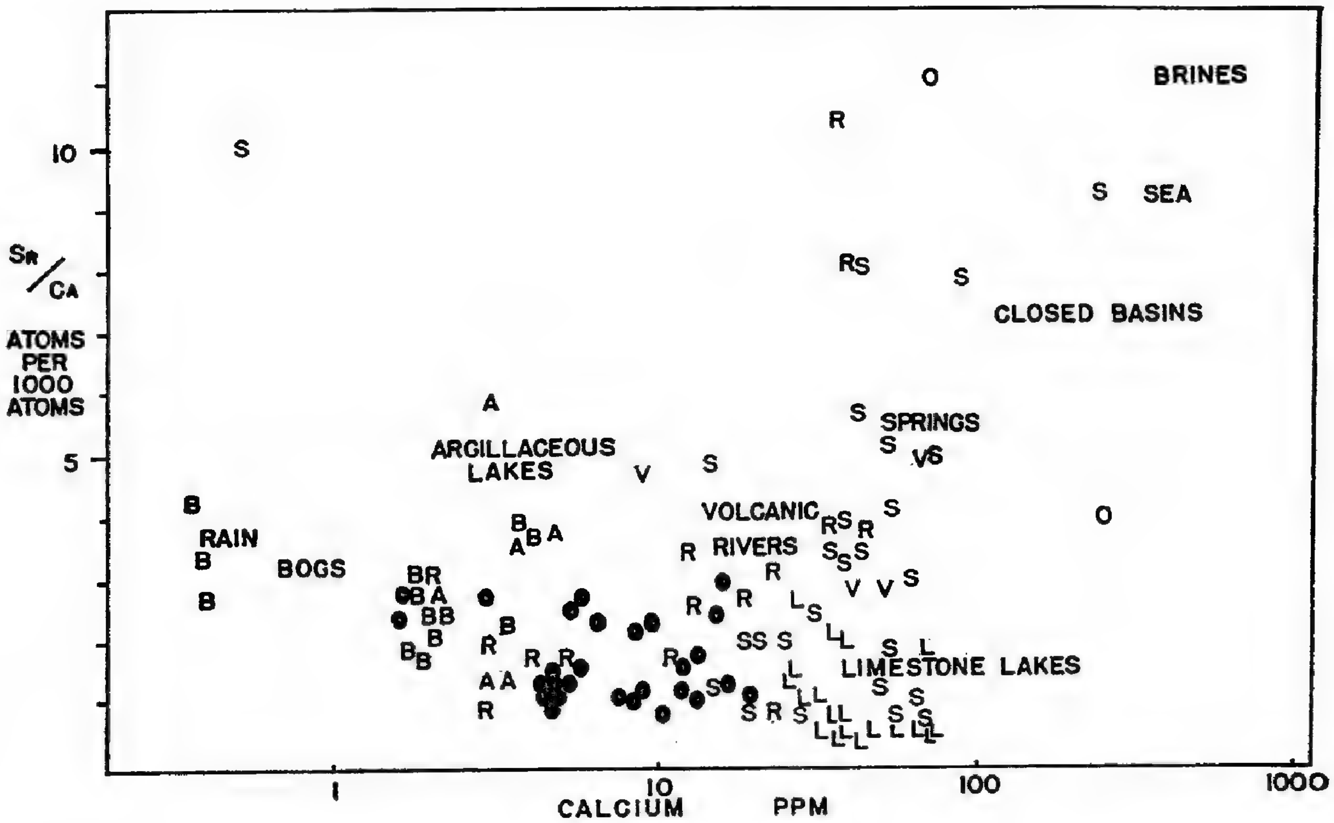

FIG. 2. Sr/Ca ratio of natural waters as a function of the calcium content. Data from this study are classified as follows: A, argillaceous lakes, turbid with clay, and low in calcium; B, bog and seepage lakes, mainly rain water, low in calcium; V, volcanic lakes; S, springs; R, rivers; L, lakes receiving drainage from old limestones; black circles are lakes with intermediate values; open circles are waters of closed lakes. Sr/Ca ratios of waters low in chloride decrease with increasing calcium content; Sr/Ca ratios of waters high in chloride increase with salinity.

in alkaline earth elements such as limestones of sedimentary origin or plagioclase, amphibole, and pyroxene of crystalline rock derivation. If the waters develop the Sr/Ca ratios of their substrates, the following patterns may be expected (Odum, 1957).

If the limestones are freshly deposited with direct precipitation involved or are made of reef coral, the Sr/Ca ratio may be as high as the sea (9.9/1000 by atoms). If, however, as is more often the case, the limestone is composed of shells of invertebrates the ratio is lower 1–6/1000 by atoms. If the limestone is replaced, especially if it is dolomitic, the Sr/Ca ratio may be much less than 1/1000. If the substrate is a soluble calcareous basic rock of non volcanic origin, a low Sr/Ca ratio is also derived (1–3.5/1000). In most calcareous substrates, high strontium contents are found with high calcium contents but the Sr/Ca ratio is low (example, Swedish lakes; Sr/Ca, 1.35 atoms/1000 atoms).

When the waters percolate non-calcareous substrates with less solubility of alkaline earth elements, a relatively larger proportion of the strontium may be derived from non-calcareous minerals which contain strontium. The larger ionic radius of strontium (1.27 A) relative to calcium (1.07 A) permits its inclusion along with potassium (radius 1.33 A) in such minerals as orthoclase feldspar as described by Noll (1934). Thus waters draining insoluble rocks tend to be low in total alkaline earths and to possess a fairly high Sr/Ca ratio (3.5 atoms/1000 atoms).

Among the igneous rocks as among the limestones there is a large range in strontium contents. Granites and other coarse grained rocks which formed slowly tend to be low in strontium, whereas rocks associated with rapid or late stages of fractional differentiations are high in strontium as in volcanic rocks or in pegmatites where strontium minerals themselves occur. Strontium more than calcium tends to remain volatile until the last stages of crystallization. Thus fine grained igneous rocks have more strontium than coarse grained rocks.

As described below in the discussion on closed basins, salt conditions, dry climates, and desert conditions tend to develop high Sr/Ca ratios so that rain percolating through such deposits will derive high ratios as well as high total concentrations.

Thus by way of summary, high Sr/Ca ratios may be expected in waters which drain evaporite deposits, pegmatites, volcanic rocks, those limestones with precipitation directly from the sea water, or fresh coral limestone. Low Sr/Ca ratios may be expected from consolidated limestones, replaced limestones, dolomites, non-volcanic basic igneous rock, and humid regions. The basis for the above summary and more complete data on the distribution of Sr/Ca ratio in regional rock types can be found elsewhere (Turekian and Kulp, 1956, Odum, 1950b, 1951a, 1957).

That the Sr/Ca ratios of surface waters actually do reflect in part the Sr/Ca of the regional substrates may be observed in Table 4. The high Sr/Ca ratios (4–10 atoms/ 1000 atoms) for western rivers of the U. S. reported by Alexander, Nusbaum, and MacDonald (1954) may be readily accounted for because of the known high strontium content of the Rocky Mountains, the widespread distribution of volcanic rock, and the arid climate. These authors also found a correlation between strontium content and the alkaline earth content of soils. Similarly the low values (mean 117 micrograms/ liter; Sr/Ca ratio, 1.3 atoms/1000 atoms) in soft acid waters in Finland reflect the low regional Sr/Ca ratio (Wilska, 1952).

TABLE 4

Comparison of Strontium in Waters and Sources

Water and Source	Sr/Ca
5 bog lakes, Connecticut and North Carolina	3.53
Possible source: rain water, 2 samples New Haven, Conn.	3.78
N. C. reservoir lake, draining residual soils on precambrian rock	3.69
Representing source: clay sediment (acid extract)	3.30
Central Connecticut lakes; drainage from Triassic shales and intrusions	1.77
Representing source: 5 soils (acid extract)	2.12
N. C. Lake Waccamaw, seepage lake with limestone outcrop	2.39
Representing source: outcrop marl	2.71
Pond with limestone outcrop, Covington, Kentucky	1.25
Representing source: outcrop limestone	1.23
37 Swedish lakes (data of Lohammar, 1938)	1.35
Representing source: Swedish rocks (Landergren, 1943)	0.3–2
Drainage from a strontianite marl dump (Haselhoff, 1893)	30
Representing source: marl from dump	7–35
Lake Wononskopomac, Connecticut, Stockbridge Marble region	1.32
Representing source: sample of bedrock dolomite	0.22
Hudson River, Poughkeepsie, N. Y., draining sedimentary area	2.65
Representing source: mean of world sediments	2.08
Philippine lakes (3) in volcanic region (see Table 17)	4.21
Representing source: rhyolite: andesite: basalt, 1:2:4 Odum (1950b), and 7 volcanic glasses	9.77
Boulder Creek, Colo. Data of Clarke (1915); Platte River draining alkali igneous Front Range of Rockies	4.2
Representing source: 78 igneous rocks from Colorado Front Range	3.1–43.0

THE TURNOVER FACTOR, CLOSED BASINS

Although the chemical constitution of a stream is largely a function of the geochemistry of the sources of water, a lake, on the other hand, has internal self-regulating systems and cycles which strongly modify the edaphically controlled properties (Hutchinson, 1948). Matter and energy pass continually through a lake, but the concentrations maintained in the lake water may be of entirely different nature from those in the inflows.

As one extreme, consider the flow of a river into a closed basin in which there is no outlet like the ocean or Great Salt Lake in Utah. As the concentrations of strontium and calcium increase in the water, the solubility product of the calcium carbonate is reached and precipitation begins. By solubility product we do not mean the chemical solubility product but the biogeochemical product which is the effective one. The calcium concentration thereafter remains constant with a steady balance between inflow and outflow. However, since most depositional processes exclude strontium selectively relative to calcium, the mineral matter being sedimented has a lower Sr/Ca ratio than the water from which it is derived. Thus strontium does not deposit as readily as calcium and its concentration in the water increases until with rising concentrations, the amount of strontium included in deposition becomes proportionately great enough to match that flowing into the basin. Eventually the Sr/Ca ratio in the sediments balances the Sr/Ca in the inflow water and an equilibrium is reached with respect to strontium, calcium and the relative amount of the two. In this state the Sr/Ca in the water of the basin is considerably higher than that in the inflowing waters as in the ocean, for example. Eardley (1938) showed the manner by which Mg/Ca ratio was maintained at a high level in the Great Salt Lake by this mechanism.

In the ocean the Sr/Ca of the sea water is about 9.0/1000 whereas the Sr/Ca ratio of representative world rivers is about 2.2/1000 (Odum, 1951a). The Sr/Ca of the Great

Salt Lake, Utah, is 4.2/1000 whereas the Sr/Ca in the inflowing rivers is 2.93/1000 (Alexander *et al.*, 1954). In another closed basin Seidell reported Sr/Ca of 11.5/1000 (Clarke, 1924).

In lakes which are not completely closed but retain the water for much longer times than do rivers, the situation is intermediate and slight increases of Sr/Ca ratio might be expected. Alexander *et al.* (1954), believed this action may have been in operation in the Great Lakes. As suggested by the Sr/Ca ratios from Lohammar (1938) in Figure 3 there was a rise in Sr/Ca ratio during a time of least turnover (August). Data from Linsley Pond, Conn. (Fig. 4) suggest a similar pattern with considerable variability.

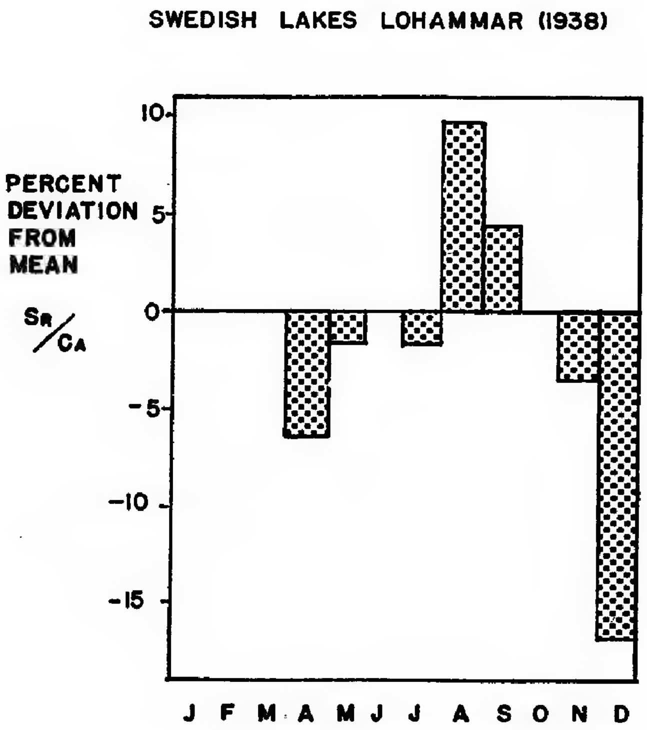

Fig. 3. Sr/Ca ratio in Swedish lakes at different times of the year based on data from Lohammar (1938). Data were not available for all months. The percent deviation of values from the mean for the particular lake is plotted. Higher Sr/Ca values occur in summer.

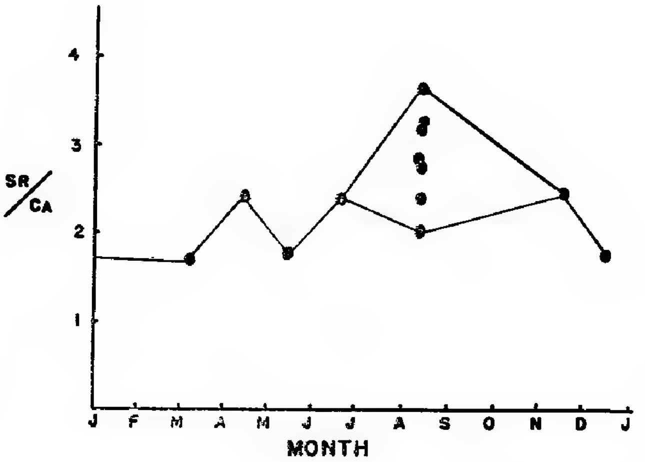

Fig. 4. Sr/Ca ratios in waters of Linsley Pond, Connecticut in 1949–50.

Illustrating the behavior of strontium during the evaporation of fresh waters is an analysis of calcium carbonate precipitate that resulted when 30 liters of water from Linsley Pond, Conn., was evaporated to 25 cc by Dr. Eva Low for another purpose. The precipitate that formed contained a Sr/Ca ratio of 1.25 atoms/1000 atoms, which is lower than most of the analyses of Sr/Ca ratio in Linsley Pond (1.65/1000) suggesting that strontium in comparison to calcium was excluded and left in the last 25 cc. Zeller and Wray (1956) found a similar increase in Sr/Ca ratio with successive precipitation.

The Sr/Ca values in closed basins will be especially high where the dilute inflowing drainage waters have high Sr/Ca ratios. For example the Lahontan Basin or the Southern California areas are much higher in strontium because of igneous, volcanic drainages than is the Bonneville basin with a predominantly sedimentary drainage.

GROUND WATER FACTOR

There are four processes which can produce higher Sr/Ca ratios in ground waters than in the surface waters from which they may be partly derived. The first process is the percolation through strata which contain pore space salt either from the ocean or from evaporite conditions in the source region. In Florida below the Suffolk Scarp at 25 ft. elevation, the land has been so recently beneath the sea that 25 to 10,000 ppm Cl still remains in the ground water (Odum, 1953; Black and Brown, 1951). As indicated in Figure 1 and Table 2, the ground waters and springs of Florida with high chloride contents have high Sr/Ca ratios, 5.7–9.3/1000. The Sr/Ca ratio for 9 Florida lakes is 2.62/1000 and for the springs including those without much chloride, 3.81/1000.

A second process which may produce higher Sr/Ca ratios in ground waters is the tendency for percolating waters to replace limestones and release strontium formerly held in the crystal lattices of the initial limestones. Evidence that this replacement process tends to lower Sr/Ca of rocks is summarized elsewhere (Odum, 1957).

A third process which may affect the Sr/Ca ratio in ground water is the differential behavior of the two elements in ion exchange processes in soils or clays. Both elements are bound by clays and organic matter. Apparently conditions exist which favor the relative retention of strontium in some cases and calcium in others. A discussion of this factor is included in the discussion of strontium content of some soils (Odum, 1957). There is little satisfactory evidence to indicate much consistent effect of soil exchange on the Sr/Ca ratio under steady state conditions.

A fourth process is the mixing of surface waters with hot solutions associated with thermal regions. Because of the high strontium content associated with vulcanism, such waters tend to have high Sr/Ca ratios.

Among mineral waters Francis (1923) found Sr/Ca 25.1/1000 and Clarke (1924) cites cases with a ratio of 28.7/1000. Such waters may have received strontium from several of these processes. M. Starr Nichols in a personal cummunication described some unusual well waters in eastern Wisconsin with 20 ppm strontium and Sr/Ca ratios up to 160 atoms/1000 atoms. Straub (1950) found up to 5.0 mg/l strontium in mineral waters. Bororik-Romonova *et al.* (1954) found 4–390 ppm.

Among waters suitable for water supply, Alexander *et al.* (1954), believed that their data did not show indication of higher strontium in ground water than in surface waters. Such waters are selected for minimum mineralization. Many of the surface waters analyzed which had high strontium were in semi-arid regions or in areas of high geochemical strontium content. In spite of this selection an average of the 21 ground water values indicates a higher Sr/Ca ratio (3.8/1000) than 50 surface water values (Sr/Ca 2.5/1000). A diagrammatic picture of the relative behavior of strontium and calcium is shown in Figure 5 where representative values of solids and waters are given. The strontium removal into ground water is shown at a rate faster than that of calcium.

CORRELATION OF SALT AND STRONTIUM

It is well known that sodium and chloride are rapidly washed out of the sediments by percolating waters and that ground waters contain higher contents of these elements than other fresh waters (Conway, 1943). Thus waters percolating unreplaced sedi-

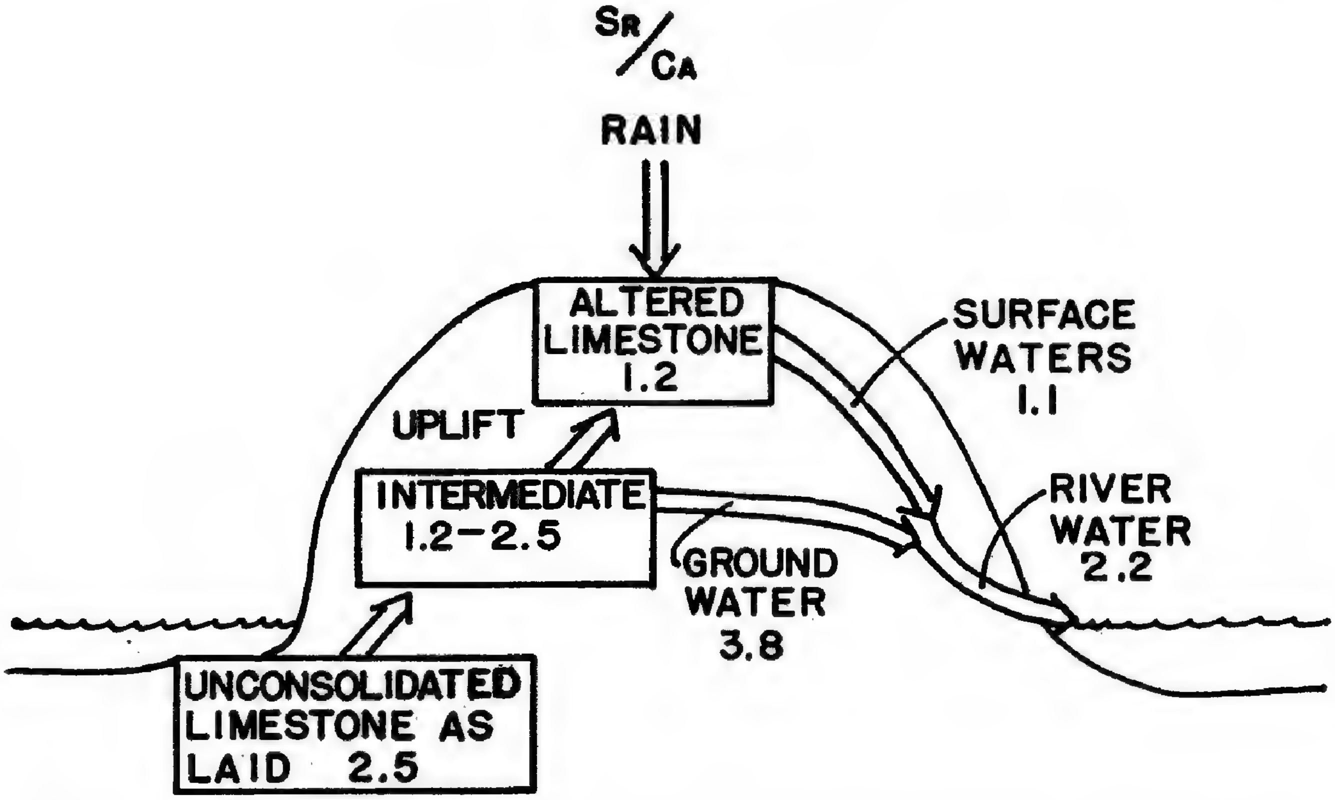

FIG. 5. The behavior of the Sr/Ca ratio in carbonate depositions during the sedimentary cycle. Values for various phases are means of data from this study. Strontium is more readily removed into solution during consolidation than calcium. This behavior accounts in part for low values af limestones and high values in ground waters.

ments like some in Florida yield high quantities of both sodium and strontium, whereas waters percolating older rocks like those in Connecticut yield lower amounts of salt and lower Sr/Ca ratios. Wherever salts of the sea or of arid basins are involved the Sr/Ca ratio tends to be high whether by direct mixture or from ancient deposits. Hydrothermal waters of volcanic regions are also rich in both strontium and chloride. Thus because of several mechanisms, there is a correlation of salt and strontium.

An example of the effect of ground-water salt in raising the Sr/Ca ratio is graphed in Figure 1. Data are plotted from the dilute ground waters of Florida (Odum, 1951c) and the brines of Kentucky (McGrain and Thomas, 1951). At salinities below that of sea water (1.9% Cl) the Sr/Ca ratio tends to decrease below the Sr/Ca ratio of sea water (9.0 atoms/1000 atoms) because of the solution of additional calcium from sedimentary rocks low in strontium. At salinities above that of sea water, the Sr/Ca ratio is observed to rise above the Sr/Ca ratio of sea water. Presumably deposition of calcium from the brines is occurring at the higher concentrations.

Regional differences in salt and strontium content are large. The difference in Sr/Ca ratio between hard waters containing salt (such as ground waters of the great plain) and hard waters low in salt (such as waters in Sweden) is striking. High Sr/Ca ratios also occur as discussed for igneous rocks where waters are very soft, or where substrates are volcanic.

Wherever waters receive little geochemical contribution but mainly elements from rain as in bog and seepage lakes a fairly high Sr/Ca ratio may be found as indicated in Table 1 for North Carolina, Connecticut, and Florida (Sr/Ca 2.0–4.5/1000). Two rainwater samples (Table 3) contained Sr/Ca ratio 3.8/1000. These moderately high values may reflect strontium of marine origin as well as of terrestrial dust origin. The widespread circulation of strontium containing dust is well known (Libby, 1956).

In surface waters close to the sea, high content of atmospheric transported salt may tend to raise the Sr/Ca ratios as it is known to do to chloride contents. It is difficult to separate this atmospheric factor from the space factor in low lying waters near the sea. In the Philippine lakes there is a volcanic factor also (Table 3).

VARIATION OF STRONTIUM IN SEA WATER

Although the strontium content of sea water seems established within small limits, the question of variation needs consideration. Sr/Ca ratios of sea water are summarized in Tables 2 and 5.

TABLE 5

Analysis of Variance in Sea Waters of Long Island Sound

Variation Source	Degrees of Freedom	Sum of Squares	Variance	Variance Ratio	Significance
Within pairs from same bottle (analytical)	61	23.5241	0.3856	1.78	sig. P.05
Bottom vs. surface[a]	1	0.0661	0.0661	10.40	none
Between months[a]	11	4.2865	0.3897	1.76	none
Residual variation (includes analytical and any unaccounted water variation)	48	33.0047	0.6876	....	....
Total	122	60.8814			
Correction of mean	1		Mean = 9.21		

[a] Unequal numbers to each subclass.

The analytical error was large as indicated by a standard deviation of 0.6209 between pairs taken from the same bottle and run on the same day; 95% of the analyses were within 13.5% of the mean. On different days and different samples the errors were larger (standard deviation, 0.6876; 95% of the analyses within 18.1% of the mean).

Analysis of variance showed no significant differences within the limits of the methods used between the Sr/Ca ratios by season, or from top to bottom water. Chow and Thompson (1955) had less variation in data obtained by direct spectophotometry from surface to 2,000 meters in 3 series including Arctic, Pacific, and Atlantic oceans. From both studies it is apparent that strontium is a conservative element with a constant ratio to other major ions.

STRONTIUM IN THE ANCIENT OCEAN

A suggested pattern of evolution of the Sr/Ca ratio during the early history of the ocean is presented graphically in Figure 6. The proposed pattern is an elaboration of the idea presented previously that the present alkaline earth cycles of the world are in a steady state (Odum, 1951a). This hypothesis should be contrasted with a recent scheme proposed by Turekian and Kulp (1956) who suggest that the Sr/Ca ratio is a function of the present igneous drainage rather than of the cyclic sedimentary drainage now prevailing in the present era (Conway, 1943).

In Figure 6 the oceanic Sr/Ca ratio is at first fairly high and charactistic of basalt drainage. Then the ratio rises to a maximum while the first calcium carbonate is precipitating because of the elimination of strontium during carbonate deposition and consolidation. Finally, the Sr/Ca ratio drops again as the uplift of sediments begins

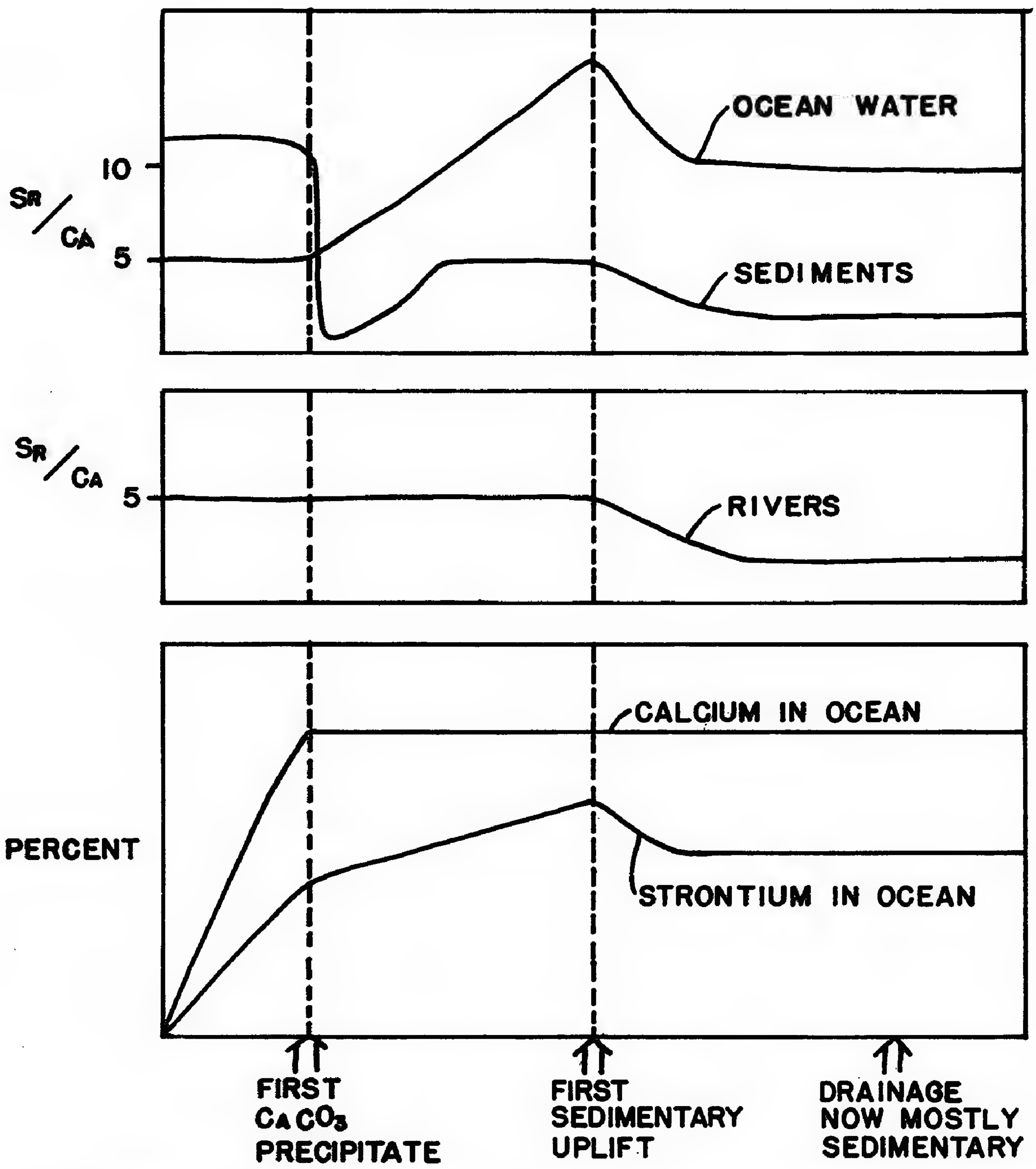

Fig. 6. A hypothesis of the behavior of the Sr/Ca ratio in the early history of the earth beginning with river drainage from a basaltic globe and an appreciable ocean with volatiles. Later a predominantly sedimentary drainage develops with a different steady state behavior of the Sr/Ca ratio. Sr/Ca ratios are given in atoms/1000 atoms.

because the rivers begin to draw much of their alkaline earth content from the uplifted sediments. By these schemes, the oceanic Sr/Ca ratio has decreased or been the same during the history of the ocean.

Summary

1. Three hundred analyses of strontium in natural waters are compared with published data in order to characterize the patterns and processes of the strontium cycle in the hydrosphere.

2. In non-marine waters, the Sr/Ca ratio of the region of water drainage is the most important factor affecting the Sr/Ca ratio of waters. Sr/Ca values range from 0.5 atoms/1000 atoms in areas draining replaced limestones to 5 atoms/1000 atoms or higher in areas of volcanic drainage.

3. Strontium is correlated with sodium chloride contents (a) because of the association of elements in waters deriving salt directly or indirectly from the sea; (b) because of the association of the elements in hydrothermal waters; (c) because of the tendency for both elements to be excluded from early sedimentary depositions and secondary diagenisis to be deposited in late evaporites. These processes tend to produce high Sr/Ca ratios in ground waters.

4. In waters of closed basins which contain a steady state balance between the substances of inflowing river and the substances sedimented, the Sr/Ca ratio develops a higher value than in basins with outflows and high water turnover.

5. A discussion of the oceanic steady state between alkaline earth inflows and alkaline earth deposition does not support recently published ideas of increasing Sr/Ca ratio in the ocean.

6. In sea water all recent studies find strontium present as a conservative element with a constant Sr/Ca ratio of about 9.0 atoms/1000 atoms (8.0 mg/1 strontium in sea water of salinity 35 parts per thousand).

LITERATURE CITED

Alexander, G. V., R. E. Nusbaum, and Norman S. MacDonald. 1954. Strontium and Calcium in municipal water supplies. J. Amer. Wat. Wks. Assn., 46: 643–654.

Black, A. P. and E. Brown. 1951. Chemical character of Florida's waters. Divisions, of Water Survey and Research, State Board of Conservation, Water Survey and Research Paper, 6: 1–119.

Borovik-Romanova, T. F., V. V. Koroler and Yu. I. Kutsenko. 1954. Spectrographic determination of strontium and lithium in natural waters. Zhur. Anal. Khim., 9: 265–269.

Bowen, H. J. M. 1956. The biogeochemistry of strontium. Advancement of Science, 12: 585–588.

Braidech, M. M. and F. H. Emery. 1935. The spectrographic determination of main chemical constituents in various water supplies in the United States. J. Amer. Wat. Wks. Assn., 27: 557–580.

Cameran, C. 1946. Composition d'une eau a forte salure du terrain houiller du Couchant de Mons. Bull. Soc. Geol. Belg., 55: 128–130.

Cartledge, G. H. 1928. Studies on the periodic system. I. The ionic potential as a periodic function. J. Amer. Chem. Soc., 50: 2855–2863.

Chow, T. J. and T. G. Thompson. 1955. Flame photometric determination of strontium in sea water. Analyt. Chem., 27: 18–21.

Clarke, F. W. 1915. Analyses of rocks and minerals, 1880–1914. Bull. U. S. Geol. Surv., 591: 1–376. 1924. The data of geochemistry. 5th ed. Bull. U. S. Geol. Surv., 770: 1–841.

Conway, E. J. 1943. The chemical evolution of the ocean. Proc. R. Irish Acad., 48: 161–212.

Delecourt, Jules. 1946. Two memorable dates in the history of the oceans. Bull. Soc. Geol. Belg., 55: 130–146.

Desgrez, A., and J. Meunier. 1926. Recherche et dosage de strontium dans l'eau de mer. C. R. Acad. Sci., Paris, 183: 689–691.

Dieulafait, L. 1877. La strontiane, sa diffusion dans la nature minerale et dans la nature vivante, a l'epoque actuelle et dans la serie des temps geologiques consequences relatives aux eaux minerales saliferes. C. R. Acad. Sci., Paris, 84: 1303.

Eardley, A. J. 1938. Sediments of Great Salt Lake, Utah. Bull. Amer. Assn. Petrol. Geol., 22: 1305–1411.

Forchhammer, G. 1865. On the composition of sea water in the different parts of the ocean. Phil. Trans., 155: 203–262.

Francis, A. G. 1923. Presence of barium and strontium in natural brines. Analyst, 48: 315–320.

Goldschmidt, V. M. 1937. The principles of distribution of chemical elements in minerals and rocks. Journal Chem. Soc. 140, pt. 1: 655–673.

Haselhoff, E. 1893. Versuche uber den Ersatz des Kalkes durch Strontium bei der Pflanzenernahrung. Landw. Jahrb., 22: 851–857.

Hummel, R. W., and A. A. Smales. 1956. Determination of strontium in sea water by using both radioactive and stable isotopes. Analyst, 81: 110–113.

Hutchinson, G. E. 1948. Circular causal systems in ecology in teleological mechanisms. Ann. N. Y. Acad. Sci. 50: 221–246.

Kulp, J. L., W. R. Eckelmann, A. R. Schulert. 1957. Strontium-90 in Man. Science, 125 (3241): 219–225.

Landergren, Sture. 1943. Geokemiska studier över Grangesbergsfaltets järnmalmer. Ingen Vetensk Akad. Handl., 172: 1–72.

Libby, W. F. 1956. Radioactive strontium fallout. Proc. Nat. Acad. of Sci., Wash., 42: 365–390.

Lohammar, Gunnar. 1938. Wasserchemie and höhere vegetation Schwedischer Seen. Symb. Bot. Upsaliens., 3: 1–252.

Lundegardh, H. G. 1929–1934. Die quantitative Spektralanalyse der Elemente. Jena, G. Fischer, 2 vols.

McGrain, P. and G. R. Thomas. 1951. Preliminary report on the natural brines of eastern Kentucky. Rep. Invest. Kentucky Geol. Surv. (Series 9), 3: 1–21.

Mellor, J. W. 1923. A comprehensive treatise on inorganic and theoretical chemistry. The alkaline earths. London, Longmans Green and Co., vol. 3, pp. 619–908.

Miyake, Y. 1939. Chemical studies of the west Pacific Ocean. The chemical composition of oceanic salt. Bull. Chem. Soc. Japan, 14: 29–35.

Noll, W. 1934. Geochemie des Strontiums. Mit. Bemerkungen zur Geochemie des Bariums. Chem. D. Erde, 8: 507–600.

Odum, H. T. 1950a. Strontium biogeochemistry, ecosystems and paleoecological tools. Report of the committee on a treatise on marine ecology and paleoecolgy, National Research Council, Washington, D. C., 10: 55–58.

1950b. The biogeochemistry of strontium, Ph.D. Thesis, Yale University, pp. 1–373 (unpublished).

1951a. The stability of the world strontium cycle. Science, 114 (2964): 407–411.

1951b. Notes on the strontium content of sea water, celestite Radiolaria, and strontianite snail shells. Science, 114: 211–213.

1951c. Strontium in Florida Waters. in Black, A. P. and E. Brown. Chemical Character of Florida Waters. Florida State Board of Conservation Division of Water Survey and Research Paper, 6: 20–21.

1953. Factors controlling Marine invasion into Florida fresh waters. Bull. of Mar. Sci. Gulf and Carib., 3: 134–156.

1957. Biogeochemical deposition of strontium. Publications of the Institute of Marine Science, 4 (2): 38–114.

Ramage, H. 1936. Biological distribution of metals. Nature, Lond., 137: 67.

Rodhe, W. 1951. Minor constituents in lake waters. Proc. Internatl. Assn. Theoret. Appl. Limnol., 11: 317–323.

Smales, A. A. 1951. The determination of strontium in sea water by a combination of flame photometry and radiochemistry. Analyst, 76: 348–355.

Straub, J. 1950. Chemical composition of mineral waters of Transylvania, their rare constituents and the biochemical importance of these. Magyar Allami Földt. Intezet, Evkönyve, 39 (1): 1–110.

Thompson, T. G., and R. J. Robinson. 1932. Chemistry of the sea. Physics of the earth, vol. 5, Oceanography. Bull. Nat. Res. Coun., Wash., 85: 95–203.

Thompson, T. G. and T. J. Chow. 1955. The strontium-calcium atom ratio in carbonate-secreting marine organisms. In: Papers in Marine Biology and Oceanography, Supplement to Deep-Sea Research, 3: 30–39.

Turekian, K. 1955. Paleoecological significance of the strontium-calcium ratio in fossils and sediments. Bull. Geol. Soc. Amer., 66: 155–158.

Turekian, K. K. and J. L. Kulp. 1956. The geochemistry of strontium. Geochim. et Cosmoc. Acta, 10: 245–206.

Vinogradov, A. P. 1938. Geochemistry and biochemistry. Uspekhi Khimii, 7: 639–686.

Vinogradov, A. P., and T. F. Borovik-Romanova. 1945. On the geochemistry of strontium. C. R. Acad. (Doklady) Sci. U.R.S.S., 46: 193–196.

Wilska, Weppo. 1952. Trace elements in Finnish ground and mine waters. A spectroanalytical study. Ann. Acad. Sci. Fennicae, Ser. A, Sect. II, 46: 1–76.

Zeller, E. J. and John L. Wray. 1956. Factors influencing precipitation of calcium carbonate. Bull. Amer. Assn. Petrol. Geol., 40: 140–152.

Biogeochemical Deposition of Strontium

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1. Introduction

In 1877 Dieulafait using a semi-quantitative flame method analyzed fossil brachiopods for strontium and concluded that because there were appreciable amounts of strontium present in modern shells and modern ocean water, similar high amounts in fossil shells must indicate that there was a high concentration of strontium in the past ocean. Thus the use of strontium as a paleoecological indicator was initiated. Many years later a new interest in the Sr/Ca ratio as a paleoecological tool developed as more quantitative methods became available (Katchenkov, 1949; Odum, 1950a, 1950b, 1951a; Kulp, Turekian, and Boyd, 1952; Lowenstam, 1954a, 1954b; Turekian, 1955; Thompson and Chow, 1955; Imbrie, 1955; Bowen, 1956; Chilingar, 1956; Turekian and Kulp, 1956; Swan, 1956). Because of the presence of a long-lived strontium isotope (Sr 90; half life, 28 years) in fission wastes, an immense literature on strontium movements in nature developed in the postwar period. Many of these tracer experiments help in the interpretation of the normal strontium cycle.

It has become clear from work done so far that a great many factors are involved in the deposition of such a trace element as strontium in minerals, skeletons, sediments, and rocks. The strontium concentration may be due to successive chemical and biological events in the cycle prior to deposition.

Strontium, like its nearest chemical relative calcium, moves from the land, down the rivers, into the seas, into the sediments and finally after depositions back to the land again with orogenic uplift. The whole pattern of this widely dispersed element constitutes a continuous cycle. Careful consideration of the properties of the overall complex gives us insight into the amount and distribution of the element at any particular time and place. This method constitutes the cycle approach to biogeochemistry. Analysis of all parts of the depositional cycle by one worker helps to eliminate false differences due to differences in methods.

If analyses of strontium-calcium ratios in ancient deposits are to yield information about paleoecological and geochemical conditions, a full knowledge must be developed of the biogeochemical strontium cycle. To this aim unpublished analyses of strontium in various phases of the earth's biosphere (minerals, skeletons, sediments, and rocks) are reported in this paper with discussion of the factors controlling the movement and deposition of strontium and with some interpretations of the use of the Sr/Ca ratio as a paleoecological tool.

A chapter on the physiological role of strontium has been omitted from publication because of the rapid development of this subject which makes any summary now premature. A partial summary is available (Vaughan, Tutt, and Kidman, 1952). This field is characterized by excessive repetition and expensive tracer work duplicating work satisfactorily accomplished years ago with analytical experiments.

ACKNOWLEDGMENTS

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An essential part of the study was the generous contribution of specimens and materials accompanied by consultation and advice. Acknowledgment of these aids follows in the text.

METHODS

Because of the diversity of soils, sediments, tissues and other materials analyzed and the dangers of interference by other ions in the flame photometric methods used, all substances other than calcium carbonate solids were extracted with acid and precipitated with excess ammonium oxalate in hot acid solutions gradually made basic. The precipitates were collected on filter paper, ashed to calcium carbonate at 600 deg. C., weighed, dissolved in 20 percent hydrochloric acid so as to make 0.1 molar calcium concentrations and finally measured on a flame photometer of home construction (Odum, 1957). Calcium carbonate samples were ashed, weighed, and dissolved in 20 percent hydrochloric acid without precipitation.

If an adequate excess of oxalate is not added, the Sr/Ca ratio decreases in the precipitate. This is expected since the solubility product of calcium oxalate (1.78×10^{-9}) is smaller than the solubility product of strontium oxalate (5.61×10^{-8}) (Joseph, 1939). For example, in three successive precipitations without excess addition of oxalate the Sr/Ca ratio diminished consecutively 0.38, 0.08, 0.06, 0.05 atoms/1000 atoms. In 5 analyses of limestones reprecipitated without excess oxalate Sr/Ca ratios between 0.19 and 0.38 atoms/1000 atoms were found. With complete precipitations Sr/Ca ratios between 0.23 and 1.10 were found. Smith and Tait (1934) removed strontium for an atomic weight determination of calcium with five successive oxalate precipitations.

In order to establish the validity of the strontium-calcium ratios made with the excess oxalate precipitation procedure, analyses were made of fragments of 6 clams *(Venus mercenaria)* with and without reprecipitation. Results are given in Tables 1–3. Analysis of variance in Table 2 indicated no significant change in the Sr/Ca ratio relative to other sources of variability. Webb (1938) failed to find strontium by arc spectroscopy of the filtrate after oxalate precipitation of sea water. Noll (1931c) indicated only 5 percent loss of strontium in oxalate precipitations. Thus within the limits of accuracy of the flame methods, the separation of strontium and calcium with excess oxalate did not seem to change Sr/Ca ratios.

The data in Table 1 when subjected to a probit test indicate a normal distribution and suitability for statistical methods. The repeated analysis of the clams on different days

TABLE 1

Technique and Variation in Analysis of Aragonite Clam Shells *(Venus)*.
Clams Increase in Size from Numbers One to Six. The Analyses on the Second Day Were Made on the Same Prepared Solutions as on the First Day. P, Prismatic layer; N. Nacreous layer. Pieces A and D Are from Older Parts of the Shell; Pieces B and C from Peripheral Younger Pieces of Shell; AB and CD from Respective Halves of One Valve.

	Reprecipitated		Direct		
	A	B	C	D	Total
First Day					
Clam 1 P	1.97	2.64	2.71	2.02	9.34
Clam 2 N	2.02	2.43	2.22	2.22	8.88
Clam 3 P	2.21	2.42	2.73	2.74	10.10
Clam 4 N	2.08	2.17	2.23	2.32	8.80
Clam 5 P	2.23	2.54	2.52	2.44	9.73
Clam 6 N	2.04	2.55	3.40	2.20	10.90
	12.55	14.75	15.80	13.94	57.04
Second Day					
Clam 1 P	2.26	2.62	2.11	2.21	9.20
Clam 2 N	2.05	2.28	2.18	2.34	8.85
Clam 3 P	2.50	2.27	2.82	3.02	10.61
Clam 4 N	2.12	1.86	2.08	2.41	8.47
Clam 5 P	2.34	2.74	2.91	2.32	10.31
Clam 6 N	2.44	2.36	3.15	2.15	10.10
	13.71	14.13	15.25	14.45	57.54

TABLE 2

Analysis of Variance of Variation in *Venus*

Variation Source	Degrees of Freedom	Sum of Squares	Variance	Variance Ratio[a]	Significance[a]
Between days	1	0.0052	.0052	5.52	None
Between pairs (spectral analysis)	23	0.6602	.0287		
Between clams	4	0.9697	.2424	1.90	None
Prismatic versus nacreous layers	1	0.3333	.3333	2.61	None
Repricipitated versus direct methods	1	0.3852	.3852	3.02	None
Between positions of pieces of clams	2	0.5807	.2903	2.28	None
Residual variation	15	1.9139	.1275	4.44	very significant
Total	48	4.8482			
Correction of mean	1	(Mean = 2.3870)			

[a] The residual variation and variation between days are compared with the between pair variation (spectral analysis). The others are compared with the residual variation, which includes the spectral analysis variation.

TABLE 3

Statistics on *Venus* Analyses

	Variance	Standard Deviation	Per Cent of of Error at P.05	P.01
Variation for *Venus* other than that due to layers and method (including component due to spectral analysis)	0.1467	0.3830	32.3	43.0
Variation due to spectral analysis	0.0287	0.1694	14.3	19.0
Variation for *Venus* not including spectral analysis component	0.0590	0.2429	20.4	27.3

indicates the level of reproducibility of the spectral analyses; 95 percent of the analyses fall within 14% of the mean (Table 3). The average error is 4.8%.

Where the crystal species was in doubt, Debye X-ray powder patterns were made. Powder was incorporated in collodion rolled threads and photographed with a copper target and a nickel filter. Identifications were made by empirical comparisons of unknown photographs with standard patterns.

In soils and sediments where large strontium contents were suspected in acid insoluble fractions, sodium carbonate fusions were carried out first in a muffle furnace. The sodium carbonate was purified by precipitating any strontium and calcium salts with ammonium oxalate, filtering, exaporating, and ashing to remove the excess oxalate. In the analyses of fused residues errors were probably greater than in other parts of the study because of the small amounts of strontium present and the possible interference and stray light in some of the reprecipitations, which still retained enough sodium to be recognizable in the flame.

In the presentation of data, analyses are given in most cases as Sr/Ca ratios as has been done by many of the previous authors. Some advantages of using ratios of two similar elements are given by Noddack and Noddack (1934). Since strontium and calcium have similar but quantitatively different solubility products and ionization constants, their behavior varies in many phases of their cycles. The Sr/Ca ratio may be used as a type of natural experiment. One element acts as a control for the other, for the ratio changes only when a process acts on the elements specifically and differentially. Concentration or dilution processes do not change the ratio. One may readily compare solutions and solids.

2. Strontium Deposition in Minerals

FACTORS CONTROLLING DEPOSITION OF STRONTIUM AS A MINOR CONSTITUENT OF MINERALS

By far, most strontium occurs as a minor constituent of minerals rather than in the two more common strontium minerals, strontianite or celestite. Historically, the occlusion of strontium has been interpreted as a substitution for some other major ionic constituent of similar ionic radius. The amount of occlusion was thought to be determined principally by the nature of the crystal lattice of the mineral. Noll (1934) correlated the distribution of strontium (ionic radius, 1.27A) with calcium (ionic radius, 1.07) and potassium (ionic radius 1.33). Thus the correlation of strontium with potassium noted by Holmes and Harwood (1932) seemed to be explained in terms of the diadochic replacement principle (Goldschmidt, 1937, Rankama and Sahama, 1950). Wager and Mitchell (1951) showed in the Skaargaard intrusion that strontium readily entered plagioclase and apatite but not pyroxene.

However, it also became clear from strontium analyses in different regions that the amount of strontium included as a trace constituent depended on factors other than the crystal structure and type of rock or mineral. Landergren (1943), Sahama (1945a, 1945b), and Lundegardh (1946) demonstrated very low strontium values for some ancient rocks of Fennoscandia in sharp contrast to high values pointed out by Hillebrand and Lundell (1929) for the front range of the Rocky Mountains in the United States. Holmes and Harwood found high values in southern Rhodesia and low values in eastern Australia. Rankama (1946) arranged analyses of granites in chronological order and noted an increase in strontium in granites since early Precambrian. He postulated the migration of elements upward to account for richer strontium contents in more recent rocks. However, ancient rocks of southern Rhodesia have high strontium contents (MacGregor, 1930, Tyndale-Biscoe, 1931). Turekian and Kulp (1956) have just published a fine summary of strontium in igneous rocks with much new data.

It thus became apparent that a major factor controlling strontium occlusion in igneous minerals is the strontium content in the solutions from which the mineral is formed. By this hypothesis the strontium content in the crystals ultimately depends on the various kinds of processes that control the movement of strontium in solutions in the geochemical cycles. Although strontium was most concentrated at a halfway point in deposition, Wager and Mitchell (1943, 1951) found an increase in Sr/Ca ratio in the Skaergaard Intrusion in Greenland, a series of rocks interpreted as representing fractional differentiation of a magma. High concentration of strontium occurs in the crystallization of pegmatites as in the Kola Peninsula (Noll, 1934; Pecora, 1942). High Sr/Ca ratios are found in the data on pegmatites given by Shimer (1943).

Holmes and Harwood (1932) and Noll (1934) noticed the correlation of strontium occlusion with rapid cooling. Thus volcanic, porphyritic, and aphanitic rocks are high in strontium in comparison to slowly-cooled, coarse grained rocks. The high strontium-calcium ratios of volcanic regions are confirmed by European data (Noll, 1934); east Indian data (Iddings and Morley, 1915) and Wyoming data (Clarke, 1915). Summaries of the strontium content in classes of igneous rocks are given elsewhere (Turekian and Kulp, 1956; Odum, 1950b). Apparently, slow crystallization permits the escape of strontium from early crystallizations finally to deposit in pegmatites or alkali rocks. The low strontium content in Fennoscandia may be due to the depth and slow crystallization of the rocks rather than to their age. The correlation of strontium with potassium may be due as much to similar behavior in being excluded from early crystallization as to similar behavior during deposition.

A clear illustration of the wide ranges in Sr/Ca ratios found within an igneous mineral of one type, apatite, deposited under different conditions is given in Table 4. Note

TABLE 4

Strontium in Phosphates

	Sr/Ca Atoms/1000 Atoms
IGNEOUS AND HYDROTHERMAL APATITES	
New Analyses	
Nepheline syenite pegmatite, Kola Peninsula	27.3
Plutonic association, Brazil	0.64
Quebec	4.16
Volcanic Rim, Tororo, Uganda	4.61
Fluorapatite, Virginia	1.82
From the Literature	
Ilmenite (Noll, 1934)	0.2
Diorite (Noll, 1934)	0.2
Gabbro (Noll, 1934)	0.2
Gabbro (Noll, 1934)	0.9
Leucite (Noll, 1934)	9.0
Kola Peninsula (Gray, 1943)	34.4
Montana (Larson *et al.*, 1952)	135
SEDIMENTARY PHOSPHATES, CONTINENTAL DEPOSITS	
Florida pebble rock[a]	1.50
Tooth in pebble rock[a]	1.85
Florida hard rock[a]	0.94
Tennessee brown rock[a]	0.77
Tennessee blue rock[a]	1.33

TABLE 4—Continued

Strontium in Phosphates

	Sr/Ca Atoms/1000 Atoms
Tennessee white rock,[a] Mary Co.	1.63
Tennessee phosphatic limestone	1.90
Idaho phosphate rock[a]	0.93
Morocco phosphate[a]	3.24
Tunis (Gray, 1943) M. Dilla	2.68
Tunis (Gray, 1943) Dyr	5.69
Egypt, Safaga (Gray, 1943) Cretaceous	0.82
Egypt, Kosseir[a]	2.92
Estonia, Tallinn[a]	5.54
Belgium, Liege, phosphatic chalk[a]	1.86
Indo China, Lao Kay[a]	2.14
S. Australia, Kapunda[a]	0.83
China, Hai Chow[a]	1.33
S. Africa, Baariids[a]	2.12
INSULAR PHOSPHATE DEPOSITS, GUANO ORIGINS	
Assumption Isle, W. Indian Ocean, in coral[a]	3.70
Rasa Island (? Okin Daito Jima—phosphatized pumice??)[a]	3.30
Curacao (Gray, 1943), on top of coral limestone and dolomite (Skeats, 1918)	0.53
Curacao[a]	1.91
Christmas Island, Indian Ocean, on top of dolomite (Gray, 1943)	0.77
Christmas Island, Malay archipelago	0.73
Swan Island soft phosphate, coral island	6.33
Chilean Guano[a]	1.15
Chilean Guano, Pabellon de Pica[b]	1.21
Anchoreta, fish eaten by Guano birds: *Engraulis iingens*[b]	1.35
Fresh Guano, Guanape Isle, Peru?[b]	1.00
Astove, Seychelles, in and on coral limestone[a]	3.18
Sonsorol, W. Pacific, thin deposit on atoll[a]	4.58
Jamaica phosphate rock[a]	1.15
Kita Daito, phosphatized pumiceous clay[a]	2.72
Walpole Island, SW Pacific, on coral rock[a]	7.78
Kusakaki Shima, Riu Kiu Islands, in coral limestone[a]	2.75
Makatea, Society Islands phosphate rock on coral rock[a]	2.24
Ebon, Marshalls, in cavities in atoll limestone[a]	7.95
Angaur, Pelew Islands, over weathered limestone[a]	1.13
Ocean Island, Gilberts, over dolomitized limestone[a]	0.95
Peliliu, Palau Islands, in limestone depressions[a]	3.04
Greenwich Islands, shallow deposits[a]	5.23
Nauru, on dolomitized coral limestone[a]	0.80
Juan de Nova Isle, Seychelles, W. Indian Ocean, grading into coral sand[a]	4.00
Sombrero Island, West Indies (Noll, 1934)	0.50
MARINE PHOSPHATIC NODULES[a]	
California 100 meters	3.47
PHOSPHATE SKELETONS SEE TABLES 6, 7, 8, 10 and 29.	

[a] Specimen furnished by S. Hendricks and K. D. Jacob.
[b] Specimen furnished by G. E. Hutchinson.

that the strontium content of apatites formed in association with pegmatites and volcanic rocks is much higher than in apatites from basic, plutonic rocks.

Some strontium is formed from radiogenic decay of radioactive rubidium but the amounts of strontium involved are minor except in minerals with very high rubidium contents (Ahrens, 1948; Rankama, 1954).

FACTORS CONTROLLING STRONTIUM DEPOSITION IN CALCITE AND ARAGONITE

Among the suggestions to account for the distribution of strontium as minor constituent in terms of lattice structure is the prediction that because of the ionic spacings and tolerances aragonite in the orthorhombic crystal system would occlude more strontium than the polymorphous mineral calcite with the same chemical composition but different crystal system (rhombohedral). Noll (1934) inferred from a half dozen analyses that more strontium was found in aragonite. Kulp, Turekian and Boyd (1952) made a similar interpretation from additional analyses of carbonate materials. Chow and Thomson (1955) made a similar conclusion from data on biological skeletons.

Because many calcites contained little strontium, Trueman (1942, 1944) postulated that the amount of strontium present determined whether aragonite or calcite formed. Faivre (1944) indicated that more than 50 percent strontium prevented calcite formation. Bloom and Buerger (1937) had presented evidence in other minerals for stabilization of structure with extraneous materials. However, questions about crystal and strontium form were unsettled because in biological depositions of calcite and aragonite, much aragonite such as in the shells of fresh water molluscs had much less strontium than that in the calcite shells of some marine species. Thus whether small amounts of strontium determined the type of crystal form or whether the amount of strontium occluded was mainly controlled by the crystal form was not certain. That the strontium correlation with crystal form does operate when other factors are equal is indicated by the Sr/Ca content of the two layers of the shell of *Mytilus edulis*. In the aragonite inner layer Sr/Ca of 3.23 atoms/1000 atoms was found whereas in the prismatic and calcite outer layer in the same animal a lower Sr/Ca of 1.96 atoms/1000 atoms was found. In shells of *Venus mercenaria* where both the prismatic and nacreous layers are aragonite, the Sr/Ca ratios were not statistically different (Table 1–3). In the grouper the aragonite otolith has a Sr/Ca ratio of 3.90 atoms/1000 atoms in comparison to a Sr/Ca ratio of 1.95 and 2.33 in the apatite jawbone and teeth.

In an effort to shed some light on the relationship of crystal form to strontium occlusion, a series of non-biological crystals of aragonite and calcite from a wide variety of localities was analyzed as given in Table 5. Just as in the case of strontium occlusion in apatite, the strontium occlusion varied greatly ranging from Sr/Ca 0.31 to 8.1 atoms/1000 atoms for calcite and from 0.61 to 15.4 atoms/1000 atoms for aragonite. In Figure 1 the frequency distribution of Sr/Ca ratios of these minerals of non-biological origin is compared with biological depositions. One concludes that although on the statistical average there is more strontium associated with aragonite than calcite, in any one sample other factors affecting the deposition are more important. Much of the correlation of low strontium content with calcite may result from the tendency for calcite to form during replacement processes which also tend to release strontium into solution.

In the needles of calcium carbonate in nudibranchs no crystal structure may be observed by means of X-rays (Schmidt, 1944; Odum, 1951c). In this isomorphous structure the Sr/Ca ratio 6–7 atoms/1000 atoms is within the range found in calcite and aragonite structures as cited in Figure 1. Lattice structure cannot be a controlling factor in this case.

Swan (1956) has pointed out in the shell of mussels the correlation of Sr/Ca ratio with rate of deposition. Just as cited in the previous discussion of occlusion in igneous processes rapid deposition does not permit the escape of a trace element as readily as does a slow precipitation. Since calcite has a somewhat lower solubility product than aragonite, the correlation of strontium with crystal form may be due in part to the tendency for aragonite to occur during more rapid depositions. The correlation of aragonite/calcite ratio and temperature found by Lowenstam (1954a, 1954b) may be functionally produced by a correlation of growth rate and temperature.

TABLE 5

Strontium Analyses of Calcite and Aragonite Crystals of Non-Biological Origin. Serial Numbers Refer to Specimens in the Brush Mineralogical Laboratory, Yale University

Specimen	Sr/Ca Atoms/1000 Atoms
CALCITE	
New Analyses	
Crestmore, California, blue with garnet, 3980	1.23
Richmond, Virginia; with trap rock, P9067	3.49
Weyer's Cove, Virginia; stalagtite, P6311	0.36
Copper mine, Lake Superior, 2260	0.31
Freiberg, Saxony, 2178	0.94
Clay Center, Ohio; interbedded with celestite	0.52
Joplin, Missouri, with dolomite, 191	0.44
Black Hills, Wyoming, from geode 396	0.58
Egrement, Cumberland, England, 455	0.25
Pargas, Finland; metamorphosed 4192	0.48
Fowler, New York, 2272	0.36
Eagle Rock, Idaho; pisolites, translucent, 2311	8.13
From the Literature	
Vein in basalt (Grahman, 1920)	0.59
Zinc mine, Franklin, New Jersey (Grahman, 1920)	0.87
Vein in arkose (Grahman, 1920)	0.02
Crystals inside fossils (Grahman, 1920)	0.82
Sove, Fengebiet, Norway, igneous (Noll, 1934)	5.0
Bervfjord, Iceland, hydrothermal (Noll, 1934)	0.10
Egremont, Cumberland (Noll, 1934)	0.5
Besarabia, Russia (Doelter, 1912)	3.1
	2.3
ARAGONITE	
New Analyses	
Eisenerz, Styria; with sulfur 2697	0.61
Tucson, Arizona; green 3987	1.74
Copper Queen Mine, Bisbee, Arizona, P6861	1.12
Alston Moore, Cumberland; fine grain, 2695	7.33
Dubuque, Iowa, 2671	3.62
Siebengebirge on the Rhine, 2650	15.8
Mine de Gyona, Rucanbunto, Silesia, 2953	5.0
Caperno, Chile, 1768	0.62
Grotta, Sicily, with sulfur, P6834	12.1
Herrengrund, Hungary, 2666	11.1
From the Literature	
21 old analyses quoted by Hintze and Linck (1930)	13.3
Girgenti, Sicily (Noll, 1934)	9
Iron carbonate nodules, middle Lias, England (Taylor, 1950)	4.4

FACTORS CONTROLLING FORMATION OF STRONTIUM MINERALS

Varied processes are responsible for the deposition of strontium minerals. In general the geochemical processes which concentrate strontium and lead to high Sr/Ca ratios in non-strontium minerals as described in previous paragraphs also produce strontium minerals. For example, there is a high strontium content in apatites from the Kola Peninsula (Table 4) where many rare strontium minerals occur in alkali pegmatites (Fersman, 1926).

Volcanic, alkali, and hydrothermal deposits contain strontium minerals especially if located in arid regions like California (Durrell, 1953). The tendency for evaporite

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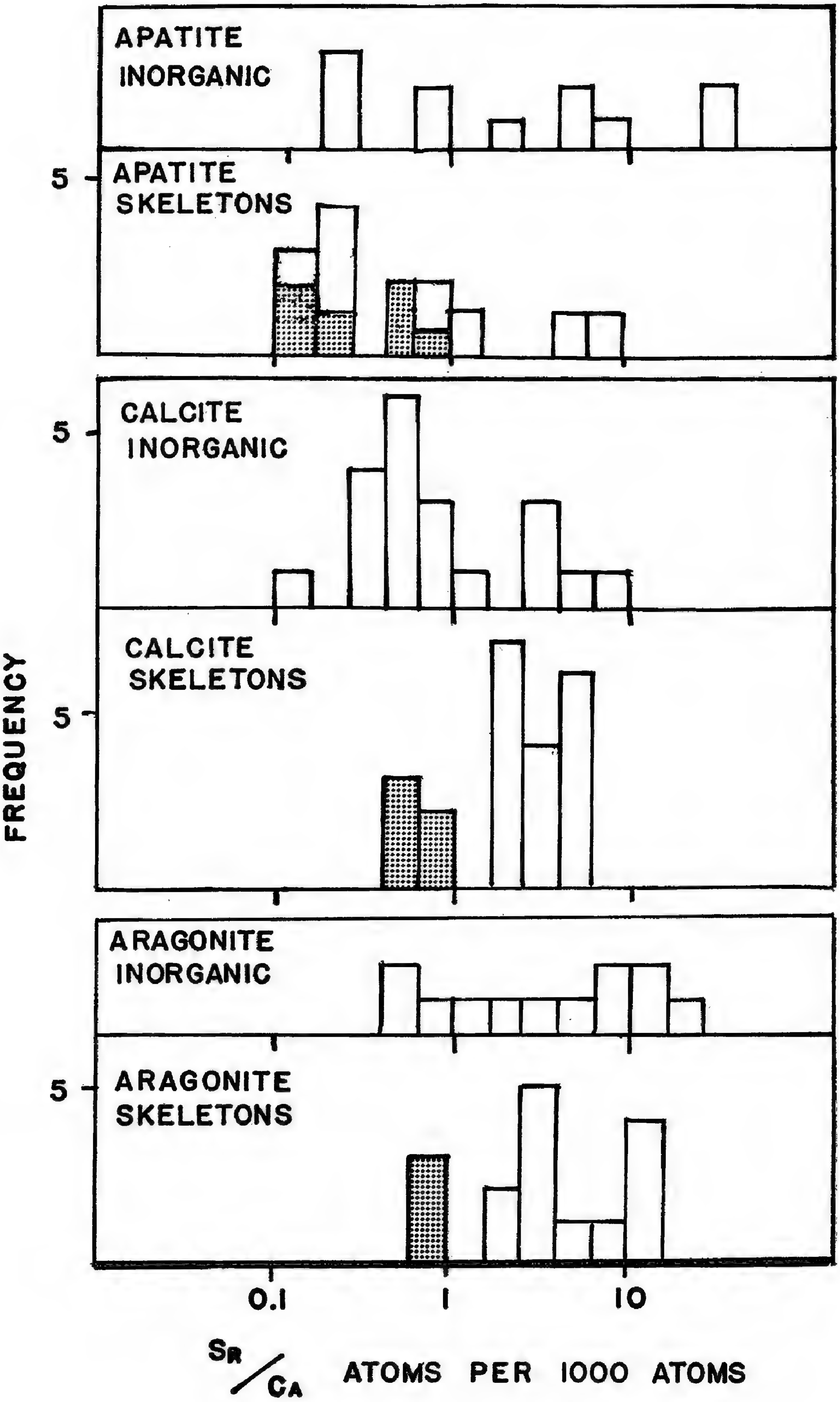
FIG. 1. Sr/Ca Ratios in inorganic crystals and biological skeletons. Frequency Distributions of Sr/Ca ratio are plotted for apatite, calcite, and aragonite. For the skeleton graphs one value is plotted for each distinct taxonomic group. The shaded data are from fresh-water; the other skeletons are marine.



APATITE INORGANIC
APATITE SKELETONS
CALCITE INORGANIC
CALCITE SKELETONS
ARAGONITE INORGANIC
ARAGONITE SKELETONS
5
5
5
5
FREQUENCY
0.1
1
10
Sr/Ca ATOMS PER 1000 ATOMS

deposits in Russia to contain strontium minerals led Vinogradov and Borovik-Romanova (1945) to postulate that strontium minerals are an indicator of arid climate at time of formation. The general absence of celestite in Florida sediments since the Eocene in contrast to the presence in sediments further west seems to agree with the climate hypothesis. Hopkins (1942) did not mention the occurrence of celestite in a study of Florida dolomites. Strontium minerals are abundantly associated with evaporite deposits in New York, Michigan, and California. In evaporites and in hydrothermal deposits there is a close association of celestite with sulfur and sulfates.

At low temperatures strontium minerals form during the replacement of limestones, dolomite, shales, evaporites, and sandstones. Many evidences indicate that the formation of celestite and strontianite in these deposits is secondary. For example, Jayaraman (1940) reports celestite encrusting ammonite casts in Madras, India. Collot (1905) reports celestite in fossil skeletons and impregnating wood. Replaced limestones in the Paleozoic formations of Ohio and New York are examples of such deposits (Stout, 1941).

There is a correlation of celestite and dolomite. As previously discussed (Odum, 1957), ground waters are relatively high in strontium, especially if there is a high salt content. Most celestite deposition in the above processes apparently comes about when such ground waters come in contact with or take up moderate sulfate concentrations. Celestite often forms in limestones along water courses and in geodes. Deposition tends to occur in porous spaces. The strontium in the percolating ground waters need not be in high concentration, for the solubility product of strontium sulfate is very small.

That high strontium concentrations are not required for celestite deposition can be determined from analysis of the strontium content of interbedded calcite and celestite crystals from a deposit at Clay Center, Ohio. The Sr/Ca ratio in the calcite was 0.52 atoms/1000 atoms, a relatively low value, indicating a low strontium concentration during the calcite formation. Yet the simultaneous crystal growth indicates that the strontium content was high enough to deposit celestite probably because of high sulfate concentrations.

Replacement of gypsum can form celestite as in Trichy, India (Jayaraman, 1940), and Germany (Linck, 1926), for strontium sulfate is more insoluble than calcium sulfate. Similarly strontianite most often forms as a replacement of celestite as at Skagit County, Washington (Landes, 1929). Dinger (1929) explained similar german occurrences by a consideration of solubility products, for strontium carbonate is much more insoluble than strontium sulfate. Aphanitic strontianite resulted from replacement phonomena in limestones and lake evaporites at Barstow, California, possibly without intermediate celestite formation. Pseudomorphs of celestite after gypsum, and strontianite after celestite have constituted proof of replacement phenomena; pseudomorphs in the reversed case have not been observed (Noll, 1934). During evaporation of saline waters, celestite apparently can deposit between the limestone-dolomite beds and the gypsum-anhydrite beds. During concentration processes the deposition of limestone-dolomite increases the Sr/Ca ratio by differential calcium and strontium deposition, so that the $SrSO_4$ solubility product, which is small, is exceeded before the $CaSO_4$ solubility product (Vinogradov and Borovik-Romanova, 1945). Apparently high salinity after limestone deposition also favors the formation of strontium minerals. Much celestite results during the formation and secondary modification of evaporite deposits as in the Carboniferous Volga dolomites.

Apparently low temperature replacement processes are involved in the formation of the celestite in the cap rocks of salt domes and with sulphur as in Texas (Wolf, 1926; Brown, L. S. 1931), Romny, Russia (Pitkovska, 1939), and Sicily (Noll, 1934); Spezia, 1895). Celestite has been found associated with the formation of lead and silver ores in Yuma, Arizona. A peculiar deposition occurred in a Japanese spring apparently owing to the sedimentation of volcanic particles (Okamoto, 1943).

Samoilov (1917, 1922) was forced to abandon an earlier hypothesis that celestite deposits of Russian Turkestan were due to biological deposition by radiolaria. There is no evidence that any natural deposits of strontium minerals are due to biological deposition. Radiolarian shales show a low strontium content (Table 24), but a high Sr/Ca ratio.

Strontium minerals also form in processes involving high temperatures. During fractional crystallization of magma the large ionic radius of strontium prevents complete incorporation into the early crystallizations and causes emanations from magma to be high in strontium (Noll, 1934). Thus strontium minerals are found in pegmatites (Fersman, 1926), contact metamorphosed structures (Lacroix, 1922), and with calcite and fluorite in a wide variety of hydrothermal veins as in Kentucky and Illinois (Grawe and Nackowski, 1949; Hardin and Thurston, 1945) or as in magnesite deposits (Matz, 1944). Rarer strontium minerals also occur in these associations (Hintze and Linck, 1930).

STRONTIUM IN ISOMORPHOUS SERIES

Although substitution of strontium for calcium or other similar ions as minor constituents is the usual pattern of distribution, the substitution of strontium in large amounts so as to form a substitution series from one non-strontium mineral to an isomorphous strontium pair apparently occurs in only a few cases. The occurrence of isomorphic series in nature is further limited because of the rarity of most strontium minerals other than strontianite and celestite. Isomorphous substitution series do occur between strontium and barium sulfates (Grahmann, 1920) and strontium and calcium silicates (Eskola, 1922; Rankama and Sahama, 1950; Toropov and Konovalov, 1943).

Complete isomorphic series between aragonite and strontianite have not been fully substantiated. One reported case turned out to be a fine grained mixture of crystals of two types separable with density solutions (Laspeyres and Kaiser, 1897). Eskola reported a substitution series without giving details. High strontium aragonite occurs as reported by Hutton (1836; Sr/Ca 40 atoms/1000 atoms). High calcium strontianites occur with atomic Sr/Ca ratios between 4.5/1 and 9.4/1 reported by several authors (Thomson, 1836; Cathrein, 1888; Knopf, 1917; Hintze, 1930). Proof of the presence of strontium and calcium in the same lattice is not available in these cases. Eyerman (1904) and Genth (1852) reported the presence of high strontium calcite but did not give supporting analyses. Zeller and Wray (1956) produced calcite precipitates with Sr/Ca ratio of 17.0 atoms/1000 atoms.

Attempts by Guichard and Wyart (1943) to produce combinations of strontium and calcium carbonates in the laboratory resulted in a 1/1 compound but no other combinations, separate crystals being usually formed. Faivre (1944) found an orthorhombic miscibility of 50 per cent $SrCO_3$ in $CaCO_3$ but only 11 per cent $SrCO_3$ in the calcite form of $CaCO_3$. Apparently the carbonate case is similar to the one for celestite and anhydrite completely worked out by Grahmann (1920) and found to have a complex phase relationship but no isomorphous series with continuous gradation of properties.

Calcium is less prevalent in celestite than in strontianite possibly because the solubility products of the carbonates are more similar. The Sr/Ca ratios by atoms range between 7.1/1 and 132/1 (Hintze, 1930; Hadding, 1939; Harness, 1949; Grahmann, 1920). In gypsum and anyhydrite the Sr/Ca ratio is between 0.05 and 25 (Noll, 1934, Clarke, 1915; Vinogradov and Borovik-Romanova, 1945).

3. Biological Deposition of Strontium

TAXONOMIC VARIATIONS IN THE SR/CA RATIO IN SKELETONS

The deposition of strontium in the skeletons of organisms is now known to be highly varied and to be affected by a great many processes related to the physiology of the organisms as well as to those factors which affect deposition of strontium in the inorganic world. The great specificity of the Sr/Ca ratio characterizing some genera, families, orders, and phyla is now established (Webb, 1937; Noll, 1934; Odum, 1950b, 1951a; Thompson and Chow, 1955; Kulp, Turekian and Boyd, 1952; Bowen, 1956). Additional unpublished data much in agreement with other published values are in-

TABLE 6

Strontium in Modern Skeletons
For Means see Table 7

Organisms	Locality	Sr/Ca Atoms/1000 Atoms
ALGAE: Calcareous skeletons		
Marine		
Calcite		
Lithothamnium and *Lithophyllum*	See Table 9	
Bossea frondifela[12]	Pacific Grove, California	3.60
Bossea corymbifera[12]	Pacific Grove, California	3.90
Corallina gracilis[12]	Pacific Grove, California	4.00
Calliathamnion sechelliae[12]	Pacific Grove, California	3.76
Calliathamnion chilosporioidea[12]	Pacific Grove, California	3.44
Aragonite		
Halimeda sp.[4]	Long Key, Fla.	10.80
Halimeda sand	Bikini[1]	13.00
Fresh water, calcite		
Chara sp.	East Twin Lake, Conn.	0.52
Chara sp.	L. Wononskopomac	0.57
Nodular type ? sp.[4]	Bass Lake, Michigan	0.49
FORAMINIFERA:		
Foraminiferal pelagic oozes, see Table 23 and Fig. 6		1.86
Calcarina defrancii	Bikini	2.77
PORIFERA:		
Calcareous sponges		
Leucetta sp.[5]	Bermuda	4.57
Scypha lingua[5]	Maine	2.79
Leucosolenia sp.[5]		4.12
Siliceous and horny sponges with calcareous inclusions, alkaline earth oxides provided by V. T. Bowen		
Dysidea crawshayi	Bermuda with shells and worm tubes	5.50
Dysidea etherea	Bimini	12.90
Dysidea etherea	Bermuda	5.18
Terpios fugax	Bermuda	3.82
Terpios zetekis	Hawaii	3.43

Chondrilla nucula	Bermuda	
Sample 1		4.46
Sample 2		2.67
Wool Sponge, Ramsey and Heath (1950)	Florida	12.0
Grass Sponge, Ramsey and Heath (1950)	Florida	1.1
Yellow Sponge, Ramsey and Heath (1950)	Florida	1.7
COELENTERATA:		
Hydrocorals:		
Millepora sp.	Long Key, Fla.	11.02
Millepora sp. (Noll, 1934)	Florida	5.00
Octocorals:		
Heliopora coerula[1]	Bikini (aragonite)	8.05
Paramuricia sp.		4.08
Tubipora sp.	Florida	4.04
Renilla sp.	Coast of N.C.	4.20
Corallium rubrum (Noll, 1934)	Sicily	2.00
Hexacorals:		
Mastipora ramosa[4]	Okinawa	10.50
Pavona dwaricata[4]	Okinawa	10.91
Pavona donai[4]	Okinawa	10.00
Seriatopora sp.[4]	Okinawa	10.20
Fungia scutari[4]	Okinawa	9.90
Seriatopora angulata[1]	Bikini Lagoon	11.20
Astreopora myriolithalmus[1]	Bikini Lagoon	11.40
Astreopora sp.[2]	Ogasawara Island	11.40
Acropora teres[2]	Bikini Lagoon	11.20
Acropora cymbicyathus[2]	Bikini Lagoon	11.21
Acropora phoronis[2]	Gardaga, Red Sea	11.05
Acropora hebes[2]	Cocos Keeling Atoll, Indian Ocean	11.19
Porites porites[2]	Dry Tortugas, Fla.	10.00
Isophyllia fragilis[2]	Bermuda	10.60
Porites clavaria (Noll, 1934)	Florida	5.00
BRYOZOA		
Retopora undata[4]	Great Barrier Reef, Australia	5.46
Retopora phoenica[4]	Great Barrier Reef, Australia	3.20
Cellopora surcularis[4]	Grand Banks	3.42
Bugula sp.	Morehead City, N.C.	3.78
ANNELIDA		
Serpulla sp.[4]	Indian River, Fla.	3.10
MOLLUSCA		
Pelecypoda		
Marine		
Pecten grandis[4]	Maine	1.87
Pecten gibbus[4]	Florida	2.08
Pecten irradian[4]	Cape Cod, Mass.	1.32
Venus mercenaria	See Table 1	
Pinna cannea	West Indies	1.39
Pinna squamosa	Naples, Italy (Noll, 1934)	0.5
Tellina dispar	Hawaii	3.3
Ensis sp.	Long Island Sound	2.57
Meleagrina margaritifera		1.70
Pholas sp.[4]	Pearl Islands	2.10
Modiolis demissa	Branford, Conn.	2.75
Vermetes sp.[4]	Bermuda	2.22
Mytilus edulis	West Haven, Conn.	
prismatic layer		1.96
nacreous layer		3.23
Mytilus edulis	(Vinogradov, 1938)	3.6
Tridacna sp.[4]		3.16
Ostrea sp.		1.33
Cavolina tridentata[4]	Atlantic	0.92
Mya arenaria[4]	Recent shell heaps, Branford, Conn.	2.72
Cardium edule	(Vinogradov, 1952)	3.6
Pelecypoda		
Freshwater		
Anodonta cygnea	(Vinogradov, 1938)	0.97
Anodonta sp.	Black Pond, Conn.	0.72
Anodonta sp.	Eastwood Lake, N.C.	0.71
Anodonta sp.	Mt. Carmel Pond, Conn.	0.47
Anodonta sp.	Roundout Creek, Rosendale, N.Y.	0.84
Anadonta sp.	Housatonic River, Conn.	0.21

TABLE 6—Continued

Stronium in Modern Skeletons
For Means see Table 7

Organisms	Locality	Sr/Ca Atoms/1000 Atoms
Anadonta sp.[5]	Devon Park Pond, Ky.	0.64
Anadonta fluviatilus[4]	Cayuga Lake, N.Y.	0.91
Anadonta sp.[4]	Fulton Co., N.Y.	0.48
Anadonta sp.[4]	Madison, Wisconsin	0.47
Anadonta gibbossa[4]	Alabama River, Ga.	0.52
Anadonta sp.[4]	Washington, D.C.	0.88
Anadonta sp.[4]	Saratoga, Ill.	0.63
Anadonta sp.	Beardsley Pond, Conn.	0.46
Sphaerium sp.	Beardsley Pond, Conn.	0.21
Musculium sp.	L. Quassipaug, Conn.	0.32
Musculium sp.	Westover School Pond, Conn.	0.75
Musculium sp.	Eastwood Lake, Chapel Hill, N.C.	0.65
Musculium sp.	Black Pond, Conn.	0.25
Elliptio sp.	L. Waccamaw, N.C.	0.98
Quadrula melanerva[4]	Cumberland R. Nashville, Tenn.	0.46
Old genus Unio, further identification uncertain:		
	Linsley Pond, Conn.	0.69
	L. Quonnipaug, Conn.	0.77
	Mt. Tom Pond, Conn.	0.38
	Roundout Creek, Rosendale, N.Y.	1.12
	Range Pond, Maine	1.02
	Sabethday Lake, Maine	0.99
	Sebago Lake, Maine	1.28
	L. Waccamaw, N.C.	1.02
	Conn. R.[4]	1.25
	Athens, Ill.[4]	0.76
	Beardsley Pond, Conn.	0.35
	East Twin Lake, Conn.	0.74
Unio pyramidatus[4]	Ohio River	1.32
Unio caurautus[4]	Sangammon River, Ill.	0.83
Unio lululensis[4]	New Zealand (arid?)	2.98
Unio lapillus[4]	Ohio	1.00
Unio securis[4]	Ohio River	1.07
Unio irroratus[4]	Ohio River	1.08
Unio perplexus[4]	Ohio River	3.35
Unio donaciformes[4]	Miami Canal, Ill.	1.03
Gastropoda		
Freshwater		
Campeloma sp.	Black Pond, Conn.	0.59
Campeloma sp.	?	0.29
Campeloma sp.	L. Waccamaw, N.C.	0.68
Campeloma sp.	Conn. River, Hartford, Conn.	0.51
Campeloma sp.	Beardsley Pond, Conn.	0.48
Campeloma sp.	East Twin Lake, Conn.	0.43
Campeloma sp.	Linsley Pond, Conn.	0.50
Ancylus sp.	Black Pond, Conn.	.25
Physa sp.	Mill River, New Haven, Conn.	0.78
Physa sp.	Wallingford, Conn.	0.14
Physa ancillaria	Roundout Creek, Rosendale, N.Y.	1.20
Physa sp.	Eastwood Lake, Chapel Hill, N.C.	1.76
Physa sp.	Beardsley Pond, Conn.	0.08
Physa sp.	Green Sink, Gainesville, Fla.	0.52
Gastropoda		
Freshwater		
Lymnaea sp.	Roundout Creek, Rosendale, N.Y.	1.17
Lymnaea sp.	Edgewood Park, New Haven, Conn.	0.50
Lymnaea columella	Cambridge, Mass.	1.11
Lymnaea emarginata[4]	Roundout Creek, Rosendale, N.Y.	6.74
Lymnaea sp.	Univ. Lake, Chapel Hill, N.C.	1.36
Ampullaria sp.[4]	Morton Lake, Lakeland, Fla.	0.81
Io spinosa	Tenn. River	1.17
Valvata tricarinata	Edgewood Park, New Haven, Conn.	1.25
Planorbella sp.	L. Wononskopomac, Conn.	0.53

Planorbella sp.	Beeslick Pond, Conn.	0.06
Planorbella sp.	Beardsley Pond, Conn.	0.28
Planorbella sp.	East Twin Lake, Conn.	0.07
Planorbis sp.	Bog Meadow Pond, Conn.	0.29
Heliosoma sp.	Middletown Reservoir, Conn.	0.21
Heliosoma sp.	L. Wononskopomac, Conn.	0.16
Heliosoma sp.	Bog Meadow Pond, Conn.	0.02
Heliosoma anceps[4]	Roundout Creek, Rosendale, N.Y.	5.27
Snail ? sp.	Inya Lake, Burma	1.94
Brackish		
Lymnaea ovata[11]	Batersjo, Baltic Sea	1.26
Terrestrial		
Helix pomatia	(Vinogradov, 1938)	2.4
Snail sp. ?	Hawaii	3.24
Snail sp. ?	El Junque, 4,000 ft. Puerto Rico	2.38
Snail sp. ?	El Junque, 4,000 ft. Puerto Rico	1.88
Marine		
Polynices sp.	See Table 9	
Littorina rudis[4]	Recent shell heaps, Branford, Conn.	2.69
Littorina littorea[4]	Recent shell heaps, Branford, Conn.	1.96
Littorina palliata[4]	Recent shell heaps, Branford, Conn.	1.86
Illyanassa obsoleta[4]	Recent shell heaps, Branford, Conn.	2.60
Anomia glabra[4]	Recent shell heaps, Branford, Conn.	1.78
Neptunea sp.	(Vinogradov, 1938)	2.4
Purpura lapillus	(Vinogradov, 1938)	2.4
Buccinum undatum	(Vinogradov, 1938)	3.4
Snail ? sp.	Massawa, Red Sea	3.60
Scaphopoda		
Dentalium pratiosum[4]	California	2.32
Dentalium sp.	(Noll, 1934) North Sea	2.00
Dentalium sp.	(Vinogradov, 1952)	2.4
Amphineura		
Chiton sp.[4]	California	10.80
Amphineura		
Chiton sp.[4]	Jamaica	7.22
Cephalopoda		
Nautilus pompilius	(Noll, 1934)	4.00
Nautilus pompilius[4]	Polynesia	3.87
Nautilus sp.	(Vinogradov, 1952)	4.8
Spirula peronii[4]		4.32
Sepia sp.[4]		6.70
Argonauta argo[4]	Sicily	4.60
ARTHROPODA		
Lepas sp.	on *Sargassum*, N.C.	6.60
Cambarus sp.	Mill River, Conn. (fresh water)	0.62
Squilla sp.[4]		6.70
Ovalipes sp.	New Haven, Conn.	7.30
Uca pugnax[8]	East Haven, Conn.	5.1
Uca pugnax[8]	Woods Hole, Mass.	5.3
Uca minax[8]	East Haven, Conn.	4.9
Menippe sp.[9]	Cedar Keys, Fla.	5.7
ECHINODERMS		
Echinarachnius sp.	Maine	2.89
Clypeaster sp.[6]	Miami, Florida	3.85
Cidaris sp.	North Carolina	2.56
Gorgonocephalus sp.	North Carolina	3.85
Schizaster fragilis[6]	Maine	2.92
Ophiura sarsi[6]	Maine	3.02
Solaster sp.[6]	Maine	4.50
Antedon sp.	North Carolina	3.38
Cucumaria sp. (body wall)	North Carolina	2.60
VERTEBRATA		
Fish Otoliths (aragonite)		
Marine		
Paralicthys americanus[7]	Long Island Sound	3.93
Paralicthys dentatus[7]	Long Island Sound	2.63
Limanda feruginea[7]	Long Island Sound	2.66
Lophius piscatorius[7]	Long Island Sound	2.05
Myax acto[7]	Long Island Sound	3.24
Hippoglossoides haleosoides[7]	Long Island Sound	2.59
Zoarces anguillaris[7]	Long Island Sound	3.60

TABLE 6—Continued

Strontium in Modern Skeletons
For Means see Table 7

Organisms	Locality	Sr/Ca Atoms/1000 Atoms
Epenephelus sp.	North Carolina	3.90
Freshwater		
Eupomotis gibbosus	Monastery Pond, Conn.	1.36
Eupomotis gibbosus	Mill River, Conn.	0.48
Erimyzon sp.	Mill River, Conn.	0.20
Fish bones and teeth		
Elasmobranchs		
Carcharias littoralis tooth	North Carolina	2.78
Squatina squatina tooth	North Carolina	2.32
Squatina squatina calcified cartilage	North Carolina	2.85
Aetobatus marinari jaw	North Carolina	1.88
Aetobatus marinari tooth		2.29
Dasyatis sp. stinger		1.98
Marine Teleosts		
Lactophrys tricornis body plate	North Carolina	2.44
Lophius sp. jaw	North Carolina	1.95
Lophius tooth	North Carolina	1.35
Seriola sp. skull and jaw		1.35
Epinephelus sp.	See Table 10	
Freshwater Teleosts		
Erymyzon sp. bones	Mill River, New Haven, Conn.	0.29
Salmo sp.	Mill River, New Haven, Conn.	0.42
Notemigonus sp. scales	Mill River, New Haven, Conn.	0.11
Lepomis gibossus bones	Mill River, New Haven, Conn.	0.17
See Table 45 also		
Reptiles, Birds, Mammals	See Tables 10 and 15.	

[1] Sample from J. Tracey.
[2] Sample from J. Wells.
[3] Sample from F. Phleger.
[4] Peabody Museum, Yale; P. Morris.
[5] Sample from W. Hartmann.
[6] Sample from W. Bergman.
[7] Sample from J. Morrow.
[8] Sample from M. Passano.
[9] Sample from E. L. Pierce.
[10] Sample from J. Brooks.
[11] Sample from G. E. Hutchinson.
[12] Sample from R. Lewin and J. Reeder.

cluded in Table 6. These analyses should be compared (Table 7) with the magnificent series of carbonate marine forms by Thompson and Chow (1955). Values by Potapenko (1925) are only semi-quantitative and those by Noll (1934) seem slightly low.

Those forms which contained appreciable phosphate were reprecipitated with oxalate and ashed prior to analysis. Carbonate forms were ashed and dissolved in acid for measurement without reprecipitation. Some mean values are given in a summary in Table 7.

In the following paragraphs some principal factors affecting the Sr/Ca ratio are considered. It will be found in the discussion that follows that the main factors controlling strontium occlusion are passive and incidental to the principal necessary functions of the organisms. Two cases where biological function of strontium exists other than as a partial replacement of calcium are: (1) in the celestite skeletons of Acantharia (See section on Acantharia), and (2) in the growth of bread mold for which functional significance has several times been reported (Lewin *et al.*, 1953; Pirschle, 1934; Steinberg, 1948).

TABLE 7

Sr/Ca in Skeletons in Relation to Taxonomic Position and Mineralogical Form

Group and Organism	Mineralogical Form	No. of Cases	Sr/Ca Atoms/1000 Atoms		Distribution Factor From Medium[a]
			This Study	Thompson and Chow (1955)	
Algae					
Lithothamnion, Lithophyllum, Bossea, Corallina, and *Calliathamnion* (marine)	Calcite	9	3.96	3.20	—2.3
Halimeda sp. (marine)	Aragonite	1	10.80	......	1.17
Fresh water algae	Calcite	3	0.52	......	—2.4
Protozoa (marine)					
Acantharian radiolaria	Celestite	1	14,300.	......	1550.
Foraminifera:				3.03	
Littoral		5	2.07	......	—4.4
Surface to 1000 M (ooze)	Calcite	4	2.61	......	—3.5
1000 M to 3400 M (ooze)	Calcite	8	1.49	......	—6.2
Calcarina defrancii, Bikini	Calcite	1	2.72		—2.9
Sponges (Calcarea) marine	Calcite	3	3.82	2.99	—2.4
For other sponges see Table 6					
Coelenterata (marine)					
Hydrozoa—Millepora sp.	Aragonite	1	11.02	8.22	1.12
Anthozoa					
Hexacoralla	Aragonite	16	10.80	9.86	1.17
Octocoralla	--------	7			
Heliopora sp.	Aragonite	1	8.06	7.57	—1.15
Others	Calcite	3	4.10	3.13	—2.25
Annellida (marine) Serpulid	Aragonite	1	3.10	5.87	—3.0
Lowenstam (1954a)	Aragonite-Calcite	30	1.4–12.0		—6 to +1.3
Bryozoa (marine)	Calcite	4	3.96	3.41	—2.3
Brachiopods (marine)					
Lingula sp.	Apatite	1	4.32	......	—2.1
Discinea sp.	Apatite	1	5.67	......	—1.6
Crania sp.	Apatite & Calcite	1	3.60	......	—2.6
Telotremata	Calcite	2	1.81	1.36	—5.1
Mollusca					
Archidoris sp.	Amorphous	1	6.75	10	—1.3
Amphineura (marine)	Aragonite	2	9.01	8.06	1.02
Mollusca					
Pelecypods (marine)	mostly Aragonite	6	2.63	......	—3.5
Pelecypods (marine)	Calcite	6	1.65	1.22	—5.6
Mytilus sp. Prismatic layer	Calcite	1	1.96	......	—4.7
Nacreous layer	Aragonite	1	3.23	..	—2.8
Pelecypods (fresh water)	Aragonite	23	0.87	0.95	—2.9
Gastropods (fresh water)	Aragonite	21	0.75	..	—3.9
Gastropods (marine)	Aragonite	8	2.31	1.68	—4.0
Scaphopods (marine)	Aragonite	2	2.35	2.35	—3.9
Cephalopods (marine)	Aragonite	3	4.86	3.75	—1.9
Cephalopods (marine)	Calcite	1	4.60	......	—2.0
Crustacea					
Cirripedia		1	6.60	4.45	—1.4
Marine Decapods	Amorphous & Calcite	8	6.03	6.17	—1.5
Fresh water Decapod	Calcite	1	0.62	......	—2.1
Insects (granules in Malpighian tubes)					
Lucilid cuprina (Waterhouse, 1950)		1	2.00	......	
Echinoderms (marine)					
Asteriodea	Calcite	2	3.71	2.73	—2.5
Echinoidea	Calcite	3	3.06	2.70	—3.0
Ophiuroidea	Calcite	2	3.47	2.69	—2.6
Crinoidea	Calcite	1	3.38	......	—2.7
Holothuroidea	Calcite	1	2.60	2.74	—3.4
Vertebrates (with some osmotic exchange)					
Teleosts (marine) bone & teeth	Apatite	6	2.33	......	—3.9
Teleosts (marine) otoliths	Aragonite	8	3.08	......	—3.0
Grouper (marine)					
jawbone	Apatite	1	1.95	......	—4.7
tooth	Apatite	1	2.33	......	—4.0
otolith	Aragonite	1	3.90	......	—2.3

TABLE 7—Continued

Sr/Ca in Skeletons in Relation to Taxonomic Position and Mineralogical Form

Group and Organism	Mineralogical Form	No. of Cases	This Study	Thompson and Chow (1955)	Distribution Factor From Medium[a]
			Sr/Ca Atoms/1000 Atoms		
Elasmobranchs (marine)					
teeth & calcareous cartilage	Apatite	6	2.35	......	—3.9
Teleosts (fresh water) bone	Apatite	3	0.82	......	—1.6
Vertebrates ,with some osmotic exchange)					
Teleosts (fresh water) otolith	Aragonite	3	0.67	......	—3.4
Amphibian (fresh water) bone					
Triturus sp., Skull,Mill R., Conn.	Apatite	1	0.10	......	—13.1
Vertebrates (with strontium and calcium through food)					
Fresh water Turtle, *Stenotherus sp.*,					
Linsley Pond, Conn.			0.57	......	....
Marine Turtle bone					
(Caretta sp.)	Apatite	1	3.29	......	—1.8[bc]
Manatee bone *(Manatus sp.)*	Apatite	1	2.33	......	—2.6[bc]
Porpoise tooth	Apatite	1	0.23	......	—10.0[b]
Guanay bone *(Phalacrocorax sp.)*	Apatite	1	0.90	......	—2.6[b]
Chamois bone *(Rupracapra sp.)*	Apatite	1	0.23	......	....
Cygnus sp. bone	Apatite	1	0.11	......	....
Canada Goose bone	Apatite	1	0.07	......	....
Chicken bone	Apatite	1	0.93	......	....
egg shell	Calcite	1	0.32	......	....
Fish eating birds, egg shells	Calcite	3	0.57	......	—4.1[b]
Invertebrate eating birds, egg shells	Calcite	2	2.40	......	2.5[c]
Newborn calf, bones and teeth					
(Rusoff, 1941)	Apatite	20	0.012	......	....
Rats (MacDonald *et al.* 1951)	Apatite	..	0.25	......	....

[a] + means enriched; — means depleted; calculated from data obtained in this study.
[b] In computing a distribution factor a fish diet is assumed with alkaline earths coming from bone.
[c] In computing a distribution factor a diet is assumed to be typical of marine tissues with Sr/Ca about 6/1000.

THE EXTERNAL SR/CA RATIO AS A FACTOR, FRESHWATER AND MARINE SKELETONS

Numerous tracer studies have shown the rapid uptake and deposition of strontium of many animals and plants when added to external media such as in deposition in worm tubes (Swan, 1950), in nudibranchs (Fretter, 1953), in tuna fish (Chipman, 1956; Ichikawa and Hiyana, 1956; Burroughs, Townsley and Hiatt, 1956) and in man (Kulp, Eckelmann and Schulert, 1957). Some of the strontium may be absorbed directly and some may be taken in as food. A proportionality between Sr/Ca ratio of external water and shells was shown for mollusks previously (Odum, 1950b, 1951a). Thus the general proportionality between the strontium content of the medium and that of skeletons of aquatic animals seems to have been established. In these as in most skeletons, there is an exclusion of strontium relative to calcium so that the Sr/Ca ratio in the skeleton is lower than that in the medium. The distribution factors indicating the factor by which the Sr/Ca ratio is lowered are given for the analyses in Table 7.

Kirchberg (1940, quoted by Sulze, 1942) caused the paravertebral calcareous sacs of frogs to dissolve and be redeposited with strontium carbonate. The frogs were placed first in acid and then in strontium solutions. The depositions were observed with a fluoroscope.

Analyses by Hodges *et al.* (1950) of human bones indicate very low Sr/Ca ratios less than values in tissues (Lundegardh and Bergstrand, 1940). Kinney and McCollum (1923a, 1923b), showed exclusion in their experiments.

Greenberg (1945) found more calcium going into bone than strontium after injections. When MacDonald *et al.* (1951) maintained a high but steady strontium diet in rats, the Sr/Ca ratio increased rapidly before leveling at a new balance with the Sr/Ca in the bone less than that in the medium.

The controlling effect of the medium is especially noticeable in comparisons between skeletons from fresh water lakes of humid regions (such as the eastern United States) and the skeletons from the sea. In Table 8 are compared Sr/Ca ratios for mollusks, algae, fish, turtles, and crustacea. The very large difference of 6 times reflects the difference between the Sr/Ca of fresh waters of about 1–3 atoms/1000 atoms (Odum, 1957) in comparison to 9.0 atoms/1000 atoms for the sea. Thus, the Sr/Ca ratio is not a taxonomic constant, but the distribution factor indicating the degree of exclusion is a taxonomic property. Only where the external medium is constant as in the sea are Sr/Ca values predictable from the taxonomic identification alone.

TABLE 8

Strontium in Fresh Water and Marine Skeletons

	Skeletons From Fresh Waters of Humid Regions		Marine Skeletons			
	Number of Cases	Mean Sr/Ca	Number of Cases	Mean Sr/Ca	Lowest Marine Value	Number of Cases Which Overlap
Aragonite Pelecypods	38	0.87	8	2.51	1.70	1
Gastropods	33	0.75[a]	14	2.34	1.70	4
Calcite Algae	3	0.58	9	3.96	3.60	0
Otoliths of fish	3	0.67	8	3.08	2.05	0
Turtle bone	1	0.57	1	3.29	......	0
Fish bones and teeth	3	0.29	13	2.29	1.35	0
Decapods	1	0.62	6	5.83	4.90	0
Mean	7	0.62	7	3.77	......	..

[a] Three very high values from one locality (Rosendale, N.Y.) were not included in this average.

THE EFFECT OF CRYSTAL FORM AND TEMPERATURE

As discussed in the section on strontium in minerals, many data from a number of authors have shown that where other factors are equal, the strontium occlusion in aragonite is greater than that in calcite. Since the crystal form in most species is a constant taxonomic characteristic, the effect of the crystal form on the occlusion of strontium tends to be constant. However, Lowenstam (1954a, 1954b) in a splendid study showed that in some forms, especially worms, the percentage of aragonite and calcite depends on the temperature. Consequently the total amount of strontium included varies similarly with crystal form percentages and thus with temperature.

For those species whose crystal form does not vary markedly with temperature, the evidence available so far suggests that there is no large variation with temperature. At least widely ranging genera and species have skeletons with similar Sr/Ca ratios in both warm and cold environments. In Table 9 there seems to be no consistent pattern with temperature in the Sr/Ca ratio in either calcareous red algae or aragonite gastropods. Kulp, Turekian, and Boyd (1952) made some similar comparisons. The strontium case is thus quite different from the case of magnesium inclusion in echinoderms (Clarke and Wheeler, 1922; Chave, 1954).

TABLE 9

Comparisons of Sr/Ca Ratio in Skeletons from Different Latitudes

Species	Locality	Sr/Ca Atoms/1000 Atoms
Polynices heros	Eastport, Maine	2.26
Polynices duplicata	Provincetown, Massachusetts	2.10
Polynices heros	Newport, Rhode Island	2.22
Polynices sp.	Long Island Sound	2.60
Polynices duplicata	South Carolina	1.70
Polynices duplicata	Florida	2.10
Polynices sp.	Florida	2.70
Polynices lactea	West Indies	2.33
Mean		2.30
Lithothamnium	Newfoundland	4.09
Lithothamnium	Orkney Islands, Great Britain	4.18
Lithothamnium	Cozumel, Mexico	4.65
Lithothamnium polymorphum	Adriatic (Noll, 1934)	3.00
Lithophyllum gardinieri	Bikini	4.10
Lithophyllum sp.	California (Thompson and Chow, 1955)	3.18
Lithothamnion conchatum	California (Thompson and Chow, 1955)	3.45
Mean		3.81

In the course of checking the crystal form on specimens analyzed, the following Debye patterns were made with results indicated. Unionid, Rosendale, N.Y., aragonite; *Elliptio*, Linsley Pond, Conn., aragonite; *Physa*, L. Wononskopomac, Conn., aragonite; *Physa*, raised in cultures high in strontium, aragonite; *Lymnaea*, Rosendale, N. Y., aragonite; *Heliosoma*, Eastwood Lake, N. C., aragonite; *Pomacea*, Lakeland, Florida, aragonite; *Scypha lingua* (Porifera), calcite; *Leucosolenia* (Porifera), calcite; *Leucetta* (Porifera) calcite; *Busycon*, aragonite; *Polynices*, aragonite; *Pecten icelandica*, calcite; *Modiolus demissa*, aragonite; *Mytilus edulis*, prismatic layer, calcite; *Mytilus edulis* nacreous layer, aragonite; *Venus mercenaria*, prismatic layer, aragonite; *Venus mercenaria*, nacreous layer, aragonite; *Archidoris*, spicules, Plymouth, England, halite in dry tissue, no lines on washed tissue, calcite on ashed tissue; nautiloid in asphalt, Pennsylvanian of Oklahoma, aragonite and calcite; *Baculites* (Nautiloid), Cretaceous, aragonite; *Tubipora* (Octocoral), Florida, calcite; *Discinea* (Brachiopod), apatite; *Uca pugnax*, calcite. Specimens were kindly provided by W. Hartmann, L. Dickie, H. W. Harvey, G. E. Hutchinson, M. Passano, J. L. Brooks, and the Bingham Oceanographic Laboratory.

The curious spicules in nudibranch tissues have now been analyzed by several authors chemically and crystallographically. They are clearly amorphous to x-rays (Rinné as quoted by Prenant, 1928; Schmidt, 1944; Odum, 1951c). Mayer and Weineck (1932) found an x-ray pattern characteristic of a mixture of vaterite and aragonite in *Doris*, but there is the possibility that these specimens had been changed by their preservation in alcohol. In *Archidoris* McCance and Masters (1938) in a nitrate separation method found Sr/Ca ratio 19 atoms/1000 atoms; Fox and Ramage (1931) found 2.3 atoms/1000 atoms in mantle with flamed paper; and Webb (1937) found 16.5 atoms/1000 atoms with an arc. Thompson and Chow found 9–11 atoms/1000 atoms. In the present study samples of *Archidoris britannica* provided by H. W. Harvey from Plymouth, England, were analyzed. 6.22 atoms/1000 atoms were found in the foot, 7.27 atoms/1000 atoms in the mantle, and 4.0 atoms/1000 atoms in the gut. Although one might relate the fairly high Sr/Ca ratio to the lack of crystal structure, the turnover factor may be responsible as discussed below.

Another possible complication in the relation of strontium inclusion to mineralogical form in skeletons is the succession of mineralogical forms during the precipitation. Mayer (1931) with x-rays, showed that the initial deposition in *Helix, Paludina,* and regeneration in *Planorbis,* was in the form of vaterite, which gradually changed to aragonite. Under proper conditions vaterite may be precipitated from solutions. On the other hand, Stolkowski (1948) also using x-rays states that the first form of calcification in *Helix* during regeneration is calcite with enrichment of aragonite with time. Crystal changes in artificial precipitates with time are well known to be very complex. Faivre (1944), for example, describes some changes for strontium and calcium carbonate precipitates. See discussions by Graf and Lamar (1955).

The existence of changes in form after the inclusion of strontium makes an understanding of strontium uptake difficult when only the final type of crystal form is known. These early changes during precipitation may be taxonomically distinctive and thus lead to taxonomically distinctive strontium content.

In the present study scrapings from the inside of valves of fresh *Elliptio* and fresh *Modiolus* were x-rayed to see if any vaterite or other crystal types were present. However, in the two cases typical patterns of aragonite were found.

In Table 11 are some analyses of the strontium, calcium, and ash contents in chelae of *Uca* during normal molting, molting induced with the removal of eyestalks, and in unmolted chelae. The chelae were obtained from L. M. Passano from his experiments in crab endocrinology. These specimens were ashed, reprecipitated, and reashed before flame analysis.

It is not known whether the lower Sr/Ca values in the unmolted chelae (4.9–5.3 atoms/1000 atoms) taken from animals in wild populations are due to a different Sr/Ca ratio in the aquatic habitat or due to a physiological difference, but the similarity of Sr/Ca ratios in the discarded and newly formed chela of the same animal suggests that deposition at different times in the hormonal cycle occurs with equal effects on strontium and calcium. If, as the fizz observations suggest, the discarded chela is mostly carbonate and the new chelae phosphate, then the mineralogical form had little effect on the Sr and Ca differentiation. There seemed to be little difference as far as differential action on calcium and strontium is concerned between normal molting and induced molting.

SR/CA RATIO IN BLOOD AND TISSUES AS A FACTOR IIN DEPOSITION

The influence of physiological systems in maintaining characteristic Sr/Ca ratios in body fluids is another factor controlling the Sr/Ca ratio in biological depositions. To gain some idea of the behavior of strontium relative to calcium within the tissues, analyses of marine and fresh water animals were made as given in Tables 10, 11, 12, and 13.

In Table 10 there is a lower Sr/Ca ratio in tissues than in the blood. The data available suggest that bloods themselves have Sr/Ca ratio approximately the same as that of the aquatic environment or slightly lower. Bowen (1956) found a Sr/Ca ratio of 11 atoms/1000 atoms in *Mytilus* tissue which was similar to that in the sea. When the tissues are grouped according to the amount of fluids present a correlation is found between strontium and fluid. The Sr/Ca ratio is highest in the aquatic medium, lower

TABLE 10

Sr/Ca Ratio in Tissues and Blood

Species and Tissue	Sr/Ca Atoms/1000 Atoms	Distribution Factor With Blood
Squatina squatina (Angel Shark)		
Whole blood	6.90	1
Centrifuged blood cells	5.70	—1.2
Muscle	2.64	—2.6
Pancreas	5.50	—1.3
Teeth	2.32	—2.9
Cartilage	3.69	—1.9
Calcified cartilage	2.85	—2.4
Epinephelus sp. (Grouper)		
Blood	6.90	1
Otolith	3.90	—1.7
Jawbone	1.95	—3.4
Teeth	2.33	—2.9
Bile (gall bladder fluid)	5.88	—1.7
Caretta sp. (Loggerhead Turtle)		
Blood	6.75	1
Bone	3.29	—2.1
Chicken		
Blood	1.35	1
Egg shell	0.92	—1.5
Feathers	1.08	—1.2
Bone	0.32	—4.2
Egg albumin	0.75	—1.8
Urine	2.20	+1.6
Libinia sp.		
Blood	9.90	1
Crustacean skeletons	6.03	—1.6
Paracentrotus lividus, data of Webb (1937)		
Coelomic fluid	15.0	1
Ovary	1.5	—10.0
Chelydra sp. (Snapping turtle)		
Blood	10.0	1
Bone	2.65	—3.8

TABLE 11

Strontium in Molting of *Uca pugnax*, Data Obtained with L. M. Passano

Stage	% Ash of Dry	% Ca of Ash	% Ca of Dry	Sr/Ca Atoms/1000 Atoms	Carbonate Qualitative Fizz Test[a]
Normal:					
Discarded chela	71.8	38.6	27.7	6.1	much
New thin chela	22.9	32.6	6.6	6.3	little
Experimental Molt:					
Discarded chela	70.8	37.6	26.7	5.8	much
New thin chela	21.9	11.0	2.3	3.0	little
Discarded chela	17.3	46.2	8.0	6.1	much
New thin chela	28.3	19.2	5.4	7.0	little
Discarded chela	58.9	44.3	26.1	5.8	much
New thin chela	28.3	15.7	4.4	7.0	little
Normal, Unmolted, wild populations:					
Uca pugnax, East Haven, Conn.	......	......	......	5.1	....
Uca pugnax, Woods Hole, Mass.	......	......	......	5.3	....
Uca minax, East Haven, Conn.	......	......	......	4.9	....

[a] Effervescence observed in acid.

in the body fluids, less in the tissues, and least in the skeletons. Thus it seems that the strontium relative to calcium is excluded somewhat in crossing from blood to tissue to intra-cellular medium. The protein materials such as mollusk operculum, muscles, and feathers have relatively low Sr/Ca values.

TABLE 12

Comparison of Sr/Ca Ratio of Marine and Fresh Water Tissues[a]
Atoms/1000 Atoms

	Polynices sp.	Venus sp.[b]	Elliptio sp.[c]
Mantle	......	3.48	2.26
Foot muscle	2.34	2.58	1.80
Adductor muscle	1.47	2.80	1.47
Gills	2.31	3.50	1.43
Visceral mass	......	3.21	2.93
Kidney	4.76	......	......
Heart	1.36	......	......
Ganglion	1.30	......	......
Digestive gland	4.54	......	......
Stomach	1.30	......	......
Opercula	2.27	......	......
Mean of tissues	2.40	3.11	1.98
Shell	2.22	2.39	0.69
Water of habitat	9.23	9.23	1.57
Distribution factors between tissue mean and water:	(—3.8)	(—2.9)	(+1.3)

[a] Great caution must be used in interpreting Sr/Ca ratios of tissues of calcareous organisms because removal from medium prevents removal of CO_2, and the resulting hyperacidity dissolves the shell, greatly changes the natural levels, and may be expected to lower the ratio also. The proof of the solvent action is contained in Collip (1920) and Dugal (1939).

[b] The *Venus* tissues collected in January, 1950 at Morehead City, N.C., were permeated by white phosphate deposits. These were separated where possible, but the values are probably affected by that which remained in the samples.

[c] From Linsley Pond, Connecticut.

Further complications are introduced when aquatic animals from quite different media are compared as is done for similar taxonomic forms in Table 12. Although the Sr/Ca of the waters differs by a factor of 6, the tissues are not so different. It appears that there is a regulation with respect to strontium. That the regulation is of importance to the animal seems unlikely; probably it is a reflection of the regulation of the other important elements. One possibility is that the fresh-water organisms do not exchange ions as often as do the marine forms so that the elevation of the Sr/Ca in the tissues that accompanies the deposition of calcium carbonate containing a low Sr/Ca is not equilibrated as rapidly by exchange with fresh solution. In any case there seems to be a real difference in the distribution factors relative to the medium for marine forms in comparison to fresh water forms. Sugehiro *et al.* (1956), found that adding calcium diminished strontium uptake in goldfish. Strontium may be taken up as a calcium replacement in fresh water more than in salt water.

In vertebrates a very extensive picture of the strontium metabolism in the body is available from many papers only a few of which indicate the relative behavior of strontium and calcium under normal and steady state conditions. In the absorption from the gut, in the deposition in skeletons, in the excretion and exchange through the gut, urine, and gall bladder strontium follows calcium somewhat but there are differential processes. No unusual mechanisms need to be postulated to account for the lower Sr/Ca ratios observed in the tissues relative to food or media. Pecher (1941) and Fay *et al.* (1942) found that the Sr/Ca ratio was lowered during uptake from the gut. In the kidney some strontium and calcium are removed and as in the case of the intestinal uptake the Sr/Ca ratio is lowered in the body and raised in the urine (Hodel, 1925; Greenberg, 1945; Pecher, 1941). There may be a similar lowering of the Sr/Ca ratio in the exchange across the placenta into developing animals (Finkel, 1947). Low Sr/Ca values have been found in the bones of newly born (Rusoff, 1941; Hodges,

TABLE 13

Sr/Ca Ratio in Tissues of Animals

Organism	Number Analyses	Sr/Ca Atoms/1000 Atoms	Distribution Factor With Calcium Source
Annelida			
Nephthys sp., Webb (1937)	1	0.91	10.1
Mollusca			
Venus sp. and *Polynices sp.* (see Table 12)	14	2.75	—3.3
Webb (1937), 6 species	7	4.4	—2.1
Elliptio sp.	5	1.97	1.2
Echinodermata			
Oreaster sp. stomach	1	4.02	—2.3
Webb (1937), 5 species	6	8.1	—1.1
Cucumaria sp.			
Retractor muscle	1	3.20	—2.9
Fat body	1	3.75	—2.5
Body wall (calcareous inclusions)	1	2.60	—3.4
Nemertean			
Lineus longissimus Webb (1937)	1	6.8	—1.4
Tunicates			
Styela sp. visceral mass, branchial basket	1	5.0	—1.8
tunic	1	6.8	—1.4
Ascidiella sp. Webb (1937) branchial basket	1	6.1	—1.5
Crustacea			
Libinia sp. blood	1	9.9	1.1
Portunus sp. eggs, from pouch	1	10.0	1.1
Eupagurus sp. Webb (1937)	1	9.1	1.0
Polyphemus sp., Crystal Lake, Wisconsin[a] 15 August, 1934	1	6.0	3.2
Tow Net plankton, L. Mendota, Wisconsin[a] 27 June, 1913	1	1.29	—1.4
Xiphosura			
Limulus sp. cuticle	1	5.6	—1.6
gills	1	3.2	—2.9
Vertebrates			
Squatina sp. (angel shark)	7	4.21	—2.2
Epinephelus sp. (grouper)	1	6.9	—1.3
Caretta sp. (loggerhead turtle)	1	6.7	—1.4
Chelydra sp. (snapping turtle)	1	10.0	....
Notemigonus sp. (fresh water)	1	0.29	—4.5
Chicken	4	1.34	....
Chicken egg albumin	2	0.93	....
Lepadogaster sp. Webb (1937)	1	1.7	—5.4
Human liver, Lundegardh and Bergstrand (1940)	..	2.3–3.1	....

[a] Samples furnished by A. Hasler.

et al., 1949; Rusoff and Gaddum, 1938). More strontium was found in stomach, urine, and oesophagus. The differential action of the body processes on the calcium and strontium has been clearly demonstrated by experiments by Hodel (1925) in which the Sr/Ca ratio of injected salts was 1:1 and in the tracer experiments of Pecher (1941) in which both strontium and calcium isotopes were used. Strontium was excreted faster than calcium and was taken up less rapidly in oral feeding. Robison and Rosenheim (1934, 1936) in vitro found that slightly higher strontium than calcium concentrations were required to produce bone deposition.

Thus slight variations in the steady state Sr/Ca ratio set up by variations in intake-excretion processes among different groups of animals may be the principle factor controlling the variations in Sr/Ca ratio of skeletal depositions.

THE FOOD CHAIN FACTOR AS ILLUSTRATED BY EGG SHELLS AND BONES

For animals such as reptiles, birds, and mammals in which the strontium and calcium are derived almost entirely from the food (rather than from exchange with aquatic media) the Sr/Ca ratio in deposition is known to be a function of the Sr/Ca ratio of the food. For example up to 10% strontium has been deposited in bones of rats fed strontium (Papillon, 1870; Konig, 1874; Stoeltzner, 1908; Kinney and McCollum, 1923a, 1923b; MacDonald, Nusbaum, Stearns, Ezmirlian, McArthur, and Spain, 1951). Wheeler (1919) and Banks and Odum (1957) obtained up to 25% strontium carbonate in egg shells by feeding strontium.

To determine further the behavior of the Sr/Ca ratio in natural food chains, analyses were made of egg shells of birds and reptiles as reported in Table 14. For marine birds two groups may be visualized: (1) those with a higher Sr/Ca ratio because their calcium comes from tissue foods only as in the case of invertebrate eaters and (2) those with a lower Sr/Ca ratio because their calcium comes from bones as in fish eaters. The Sr/Ca ratio of tissues is higher than the Sr/Ca ratio of bones (Table 10) and the egg shells might be expected to reflect this difference in food. This is a possible explanation for the differences in Table 13 between the low values (0.28–1.54) of the penguin-cormorant group and the higher values of the albatross. In the case of the terrestrial birds there is apparently little difference between the herbivorous birds and the birds which feed mostly on insects. With the terrestrial hawks, however, the lower Sr/Ca ratio observed (0.20–0.70 atoms/1000 atoms) suggests that their source of calcium has a lower Sr/Ca ratio. They may absorb some bone material from their vertebrate type food even though most of it may be cast out in pellets.

A comparison of the Sr/Ca of the bones of some marine vertebrates is presented in Table 15. The kelp goose has a higher Sr/Ca than the Canada goose but the difference is not as great as might be expected if the kelp goose were getting all its calcium and strontium from kelp, a brown alga with high strontium (30 atoms/1000 atoms). The *Cygnus* and Canada goose have quite low values possibly because of their fresh water affiliations. The Guanay has a moderately low value possibly because of its fish diet.

The porpoise with its dietary source of calcium being fish bones, has a low ratio. The fish-eating groups get their calcium more directly from the sea at least in part. The manatee and loggerhead turtle presumably have plant and animal tissue diets not containing much bone giving a relatively high Sr/Ca ratio to their source of calcium. If this reasoning is correct the fossil *Icthyosaur*, *Hyposaurus* and amphibium *Eryops* obtained their calcium by exchange or from diets predominately of tissues. There are other possibilities.

TABLE 14

Sr/Ca Ratio of Bird and Reptile Eggshells Relative to Diet and Region

Habitat and Food Habits	Sr/Ca
Marine Birds:	
Invertebrate diet:	
Diomeda exulans	2.21
Actitis macularia (fresh and marine)	2.60
Actitis mascularia Florida	1.02
Rynchops Nigra Florida	0.93
Diet with some fish:	
Ardia herodias	1.15
Uria lomvia	1.74
Alca torda	0.64
Fish diet (much calcium in fish bones with low Sr/Ca ratio):	
Phalacrocorax auritus Florida	1.54
Phalacrocorax auritus	0.35
Nycticorax nycticorax (fresh or marine)	0.75
Rock Hopper Penguin	0.62
Pandion halioetos	0.28
Continental Birds:	
Herbivores—at least partly; Sr/Ca ratio in plants fairly high:	
Melospiza melodia	0.76
Pooecetes gramineus	0.90
Fulica americana	0.50
Molothrus ater	0.83
Branta canadensis	0.86
Pigeon	0.57
Gallinula chloropus	0.67
Pipilo erythropthalmus, Florida	0.25
Anhinga anhinga, Florida	0.26
Mean	0.62
Invertebrate Carnivores:	
(Calcium from tissues or water; the invertebrates obtained their tissue calcium from plants and water)	
Charadrius vociferus	0.86
Icterus galbula	0.95
Hirundo rustica	0.81
Contopus virens	0.35
Myiarchus crinitus	1.45
Ixobrychus exilis	0.36
Colinus virginianus (at nesting season)	0.75
Colinus virginianus, Florida	0.30
Colaptes cafer, California (a high Sr/Ca area)	3.31
Toxostoma rufum, Florida	0.30
Agelaius phoeniceus, Florida	0.54
Falco sparverius, Florida	0.50
Chordeiles minor, Florida	0.92
Tyrannus dominicensis, Florida	0.83
Mean	0.71
Carnivores—vertebrate food, thus high in food chain:	
Buteo imaicensis	0.35
Buteo platypterus	0.35
Accipiter cooperii	0.40
Accipiter cooperii, Florida	0.70
Otis asio, Florida	0.40
Bubo virginianus, Florida	0.23
Buteo lineatus, Florida	0.67
Buteo brachyurus, Florida	0.20
Mean	0.37
Reptiles	
Alligator, Florida	1.10
Snake, Florida	0.70
Snake, Florida	0.65
Turtle, Florida	0.43

TABLE 15

Strontium in Marine Vertebrate Skeletons

	Sr/Ca Atoms/1000 Atoms
Fishes	
Elasmobranchs	2.35
Teleosts	2.33
Reptiles	
Loggerhead turtle	3.29
Icthyosaur, Jurassic	3.41
Hyposaurus, Cretaceous	2.05
Birds	
Kelp goose (*Chloephaga hybrida*)[a]	0.71
Canada goose (*Branta canadensis*)[b]	0.07
Cygnus, west Africa[b]	0.10
Guanay, from guano deposit[b] (*Phalacrocorax bougainvillei*)	0.90
Marine Mammals	
Manatee	2.33
Porpoise	0.23

[a] Sample from J. Delacour

[b] Sample from J. Gregory.

STRONTIUM TURNOVER AND ISOLATION OF DEPOSITIONAL SURFACES AS A FACTOR IN DEPOSITION

Although tissue, mineralogical, and food chain differences in the process of transfer of strontium and calcium from the aquatic medium through the body and into varying crystal structures may account for some of the differences in characteristic Sr/Ca ratios in different species, none of the processes presented so far seem to account in a reasonable way for the observed Sr/Ca ratios that are so high in reef corals and amphineurans and so low as pelagic foraminifera and filter feeding pelecypods or brachipods.

A partial answer may be found in the same phenomenon inside organisms that occurs in the sedimentary cycle of closed basins. The exclusion of strontium from the crystal deposition tends to raise the Sr/Ca ratio in the surrounding tissues. If deposition takes place under a steady state condition which involves little free ionic exchange with the external medium, the Sr/Ca ratio will be higher both in the tissues immediately around the deposition and in the deposition itself. If there is free exchange with the environment, the Sr/Ca ratio of the immediate chemical environment of the deposition will be little altered by the deposition and a steady state condition will result with the lower Sr/Ca ratio both in deposition and surrounding tissue. Rapid depositions or slow exchange will tend to raise the Sr/Ca issue as noticed by Swan (1956). Rapid circulatory systems, efficient excretory systems, planktonic existence, all tend to lower the Sr/Ca ratio by this prediction. On the other hand deposition in enclosed places deep in tissues not closely connected with exchange membranes will lead to higher Sr/Ca ratios.

To check this idea, some characteristic Sr/Ca ratios of marine groups were plotted on a semi-quantitative graph with two coordinates: (1) thickness of tissue separating the calcification from the sea and (2) estimated effectiveness of internal circulation mechanisms. Then lines of equal Sr/Ca ratio were drawn. The result is Figure 2. That it is possible to draw somewhat concentric isopleths separating the exposed, well-circulated deposition tissues with low Sr/Ca ratio from the restricted, little-circulated depositions seems to be evidence for the workings of the exchange theory in controlling the Sr/Ca ratio. Borroughs, Townsley, and Hiatt (1956) found that strontium

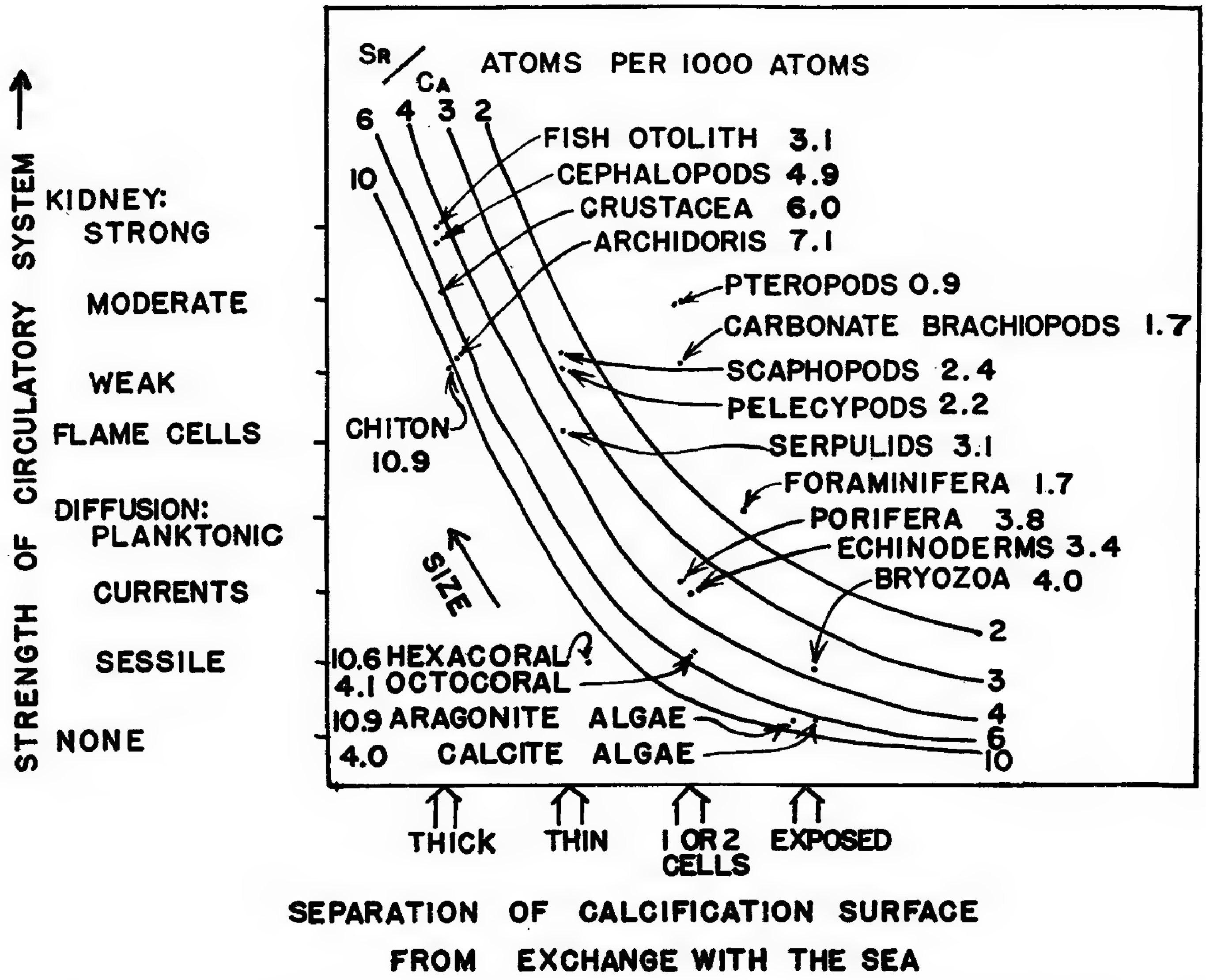


FIG. 2. A semi-quantitative graph relating the Sr/Ca ratio of skeletons of various groups of organisms to the rate of turnover of substances in the depositional tissue. The vertical coordinate is the strength of the excretory and circulatory systems of the organism ranging from no circulation to a strong kidney. The horizontal axis is the thickness of the tissue separating the calcification surface from the sea. An effort has been made to draw isopleths of approximately equal Sr/Ca ratio. Species with poor exchange due to poor circulation and thick separation from the sea in the lower left corner of the diagram seem to have high Sr/Ca ratios. Species with exposed calcification surfaces and good circulation provided either internally or due to planktonic existence are in the upper right side of the diagram and are characterized by lower Sr/Ca ratios.

turned over most rapidly in those tissues of tuna fish best supplied with blood circulation. Liver and kidneys had a high turnover rate; muscle had somewhat less turnover. Grosch and LaChance (1956) found especially high strontium turnover rates in the wasp *Habrobracon.*

Some of the characteristics of groups may be related to the properties of exchange. Echinoderms uniformly lack an internal circulatory system and have very uniform Sr/Ca ratios. Mollusks on the other hand have very diverse patterns of circulation and have diverse Sr/Ca ratios. There are very high strontium values in those corals which also have symbiotic green algae and zooxanthellae. If skeleton formation in corals takes place under the internal rising pH of photosynthesis during the day when tentacles are retracted, there may be much more rapid deposition than exchange so that all alkaline earths are precipitated in situ. The lower Sr/Ca ratios of non-photosynthetic corals thus may have an explanation. The correlation of aragonite with the algal tissue in corals may also be involved.

SR/CA RATIOS IN PLANTS

Partly because of a similarity of ionic potentials (Hutchinson, 1943) strontium is like calcium and enters plant cells by diffusion under conditions of exchange, becoming largely bound within the plant tissues (Jacobsen and Overstreet, 1947; Spooner, 1949). The principal factor controlling the strontium in the tissues is the concentration in the soluble alkaline earth fraction around the cells or around the roots (Stoddart, 1876; Haselhoff, 1893; Mazia, 1940; Collander, 1941a; Fretter, 1953; Rediske and Selders, 1953; Kraus and Porter, 1954; Rice, 1956; Bowen and Dymond, 1955, 1956). The Sr/Ca ratio within the tissues is in a few cases different from that outside, sometimes being much greater as in brown algae (Spooner, 1949) and lower as in some green algae (Table 17). One finds by recalculations on data from Collander (1941) that in low strontium concentrations the Sr/Ca was slightly raised during uptake whereas when strontium and calcium were equally concentrated, the Sr/Ca was lowered. Romney, Rhodes and Larson (1954) also found that more strontium was taken up when

TABLE 16

Sr/Ca Ratio in Plants in Relation to Sr/Ca Ratio of an Acid Bog Substrate (pH 4.5)
Singletary Lake, North Carolina

Material	Calcium % of Dry	Sr/Ca Atoms/1000 Atoms	Distribution Factor From Water
Lake water, 0.35 mg./l. calcium	......	3.50	.....
Lake peat—fine grained Du	1.60	3.06	1.15
Fibrous, peripheral peat	0.012	5.80	1.65
Persea borbonia, leaves	0.20	10.8	3.09
twigs	0.29	9.0	2.57
Taxodium ascendens, leaves	0.54	2.63	—1.33
bark	0.052	3.20	—1.09
wood	0.033	3.73	1.05
Nyssa biflora, wood	1.27	2.90	—1.21
bark	1.59	3.42	—1.02
Chamaecyparis sp., twigs	0.35	3.57	1.02
Sphagnum (in water)	0.009	6.97	2.00
Acer rubrum	0.68	4.20	1.20
Means	.55	4.94	1.53

TABLE 17

Sr/Ca Ratio in Marine Algae

	Sr/Ca Atoms/1000 Atoms	Ca % of Dry	Ca % of Ash	Distribution Factor
Algae				
Brown Algae				
Laminaria agardii	40.3	1.29	4.99	4.4
Ascophyllum nodosum	29.8	1.64	6.10	3.2
Sargassum (pelagic)	42.9	......	21.7	4.6
Fucus serratus (Webb, 1937)	45	......	......	4.9
Fucus, from Baltic	25.6	......	......	2.8
Saccorhiza bulbosa (Webb, 1937)	45	......	......	4.9
Green Algae				
Ulva lactuca	6.8	0.37	1.38	—1.4
Ulva lactuca (Webb, 1937)	3	......	......	—3.1
Red Algae				
Chondrus crispus	9.3	0.39	1.75	1.0
Ceramium sp.	3.9	0.40	1.43	2.4

calcium concentrations were low. Rice (1956) found similar results in *Carteria,* a green alga.

The actual process of uptake of the strontium seems to be as complex as has been demonstrated for other ionic uptake. Krogh (1946) and Lowenhaupt (1956) present good statements of alkaline earth uptake as a result of energy releasing steady states. Experimental studies illustrate some of the complexities affecting the Sr/Ca ratio in plants.

Stoddart (1876) reported strontium rich plants growing on celestite rich marls. Haselhoff (1893) grew beans and corn in high strontium solutions. Strontium was enriched during uptake 1 to 4 times in corn and 10 to 440 times in the beans. Higher strontium was accompanied by increasing enrichment of strontium relative to calcium in the uptake. Sr/Ca values between 10 and 106 atoms/1000 atoms were reported.

Molisch (1923) found cystoliths of *Goldfussia isophylla* or *Fiscus elastica* forming on the surface of the plant as little sphaerites. Strontium oxalate crystals form in *Begonia vitifolia* grown in strontium nitrate solutions. Miyake (1914) found strontium partly replacing calcium in rice plants on alkali soils. Rusoff, Rogers, and Gaddum (1937) found smilar strontium contents in Florida wire grasses raised under different conditions with respect to time of recent burning.

Collander (1930, 1936, 1937, 1939, 1940, 1941a, 1941b) studied strontium uptake in *Chara* and other plants. There was slight strontium accumulation in the cell sap. In growth during 12 days strontium uptake was stimulated by light, new alkaline earth elements being taken up only by growing cells. Collander believed there was strontium pectinate binding. There was a higher percent of calcium, strontium, and lithium in shoots than in roots. In 21 plants grown in 0.001M $CaCl_2$ and 0.001M Sr/Cl_2 mixtures the plants contained a Sr/Ca ratio of 1–2 atoms per atom; plants grown in solutions with a wide range of Sr/Ca ratio (0.4–739 atoms/1000 atoms) contained Sr/Ca ratio similar to the medium.

Mazia (1938a, 1938b) studied uptake of strontium and calcium in *Elodea* with subsequent deposition in vacuoles as crystals of oxalate. With Sr/Ca in a 1:1 atomic ratio strontium tends to replace calcium. Sodium present as 0.1M concentration prevents uptake of strontium from 0.0005M solution. Without the sodium the strontium is taken up.

Ramage (1936) has compared the deposition of mineral elements in the shedding of leaves and seeds to excretion in animals.

Albrecht and Schroeder (1942) found more strontium taken up when the soil was acid. Nishita, Kowalewsky, and Larson (1956a) found organic matter decreased radioactive strontium uptake although dilution of the tracer strontium by the ions in the organic matter may have been involved. Menzel (1954) found less radioactive strontium taken up when more exchangeable calcium was present. In Menzel's study also, results are uncertain because the non-radioactive strontium variation was unknown. Smith (1944) found radiostrontium uptake localized in the chloroplasts and vacuoles. Walsh (1945a, 1945b) found more strontium in the heads of oats than in other grains.

Jacobsen and Overstreet (1947) found that radiostrontium was taken up in roots within a few millimeters of the tip distal to the root hairs. The strontium was found in an exchangeable form being released most easily when dead. The uptake was more rapid in the living. A temperature range of 25 degrees caused 15 times variation in rate of uptake.

Spooner (1949) showed that radiostrontium was taken up by exchange and bound. This uptake was found to be selective with strontium being enriched over calcium by differential binding in the brown algae but not in the reds and greens.

Spinks, Cumming, Irwin, and Arnason (1948) found that radiostrontium in seeds was concentrated in the first two leaves during germination. Bastin and Trimble (1896) found 1 percent strontium in red clover over strontium rich fertilizer. Robinson, Steinkoenig, and Miller (1917) found Sr/Ca ratio 11 atoms/1000 atoms in miscellaneous Angiosperms and 0.68 in pine needles and stems. Hutchinson and Wollack (1943) found 1.2 atoms/1000 atoms in the Pteridophyte, *Lycopodium*. Ramage (1936) found 1.4–2.4 atoms/1000 atoms in apples and 3.3–6.8 atoms/1000 atoms in rubber tree seeds; Tate and Whalley (1940) found 4–8 atoms/1000 atoms in tobacco.

Bowen and Dymond (1955, 1956) found strontium rejected slightly in analyses of Sr/Ca of plants relative to their natural soil substrates. Some very high Sr/Ca values were found in a particular location near Bristol and in *Arabis stricta*.

In algae Rice (1956) found strontium uptake required living conditions in a green algae *(Carteria)* and was proportional to division rate of the cells. Whether a 1,600-fold concentration in *Carteria* represented concentration of both strontium and calcium or selective retention was not made clear. In *Chlorella pyrenoidosa* Knauss and Porter (1954) found in tracer experiments that strontium was concentrated about 10 times more than calcium.

Still unexplained is the high strontium content of the brown algae. Forchhammer (1844) found a high strontium content in *Fucus*. As was shown first by Webb (1937), such brown algae are 4–5 times higher in Sr/Ca ratio than the medium and have a ten times higher absolute concentration of calcium than the sea water although the tissue salinity is similar to that of the water. Wilson and Fields (1942) found 2% strontium in the ash of Macrocystis. Hutchinson, Seltow, and Brooks (1946) found high values in Sargassum. Because of the absolute enrichment as well as the increase in the Sr/Ca ratio, base exchange binding has been suggested. Wasserman (1948) presented this point of view and actually treated shredded *Ascophyllum* as a chromatographic column and extracted with acid before passing through a calcium solution. The algal tissues behaved in a similar manner to peat or soils. Spooner (1949) demonstrated a base exchange behavior by using Sr radioactive isotopes. The curve of uptake was similar to exchange curves, and the strontium in the algae was not lost when put into distilled water. Strontium therefore could enter or leave the algal tissue only if there was an exchange with other atoms. The fact that Wasserman used acid prior to exchange experiments suggests that the cells were dead. A proof that the base exchange mechanism is the complete answer requires an isolation of the exchange compounds involved. A solution of strontium and calcium chlorides in Sr/Ca ratio 22 atoms/1000 atoms was passed through a sample of alginic acid on filter paper in a funnel. After washing, both the alginic acid and filtrate were analyzed; both Sr/Ca ratios were the same. Apparently the differential binding is not due to alginic acid.

In the present study some analyses were made of two groups of plants growing naturally in media of known Sr/Ca ratio (1) algae in the sea, a high calcium environment; (2) trees in a peat bog of Singletary Lake, Bladen County, North Carolina, a low calcium environment. These analyses given in Tables 16 and 17 agree with previous work in indicating a high concentration factor in Sr/Ca ratios in the brown algae but little if any variation in Sr/Ca ratio relative to the medium in the other plants measured. An increase in Sr/Ca ratio was observed in the bay trees, and some slight exclusion of strontium was found in Ulva although less than that reported by Webb (1937). It is likely that a wide range of Sr/Ca ratios will be found in plants because of the wide variety of possible compounds in plants which may retain strontium and calcium selectively.

ACANTHARIA

Quite in a class by themselves are the Acantharia whose skeletons are composed of celestite. One species of *Acanthometra* dominates the plankton sample pictured in Figure 3. A predominance of celestite ($SrSO_4$) in these skeletons was reported previously on the basis of x-ray and chemical analyses (Odum, 1951b). This sample was discovered by Georgiana Deevey and Grace Pickford, members of the Bingham Oceanographic laboratory.

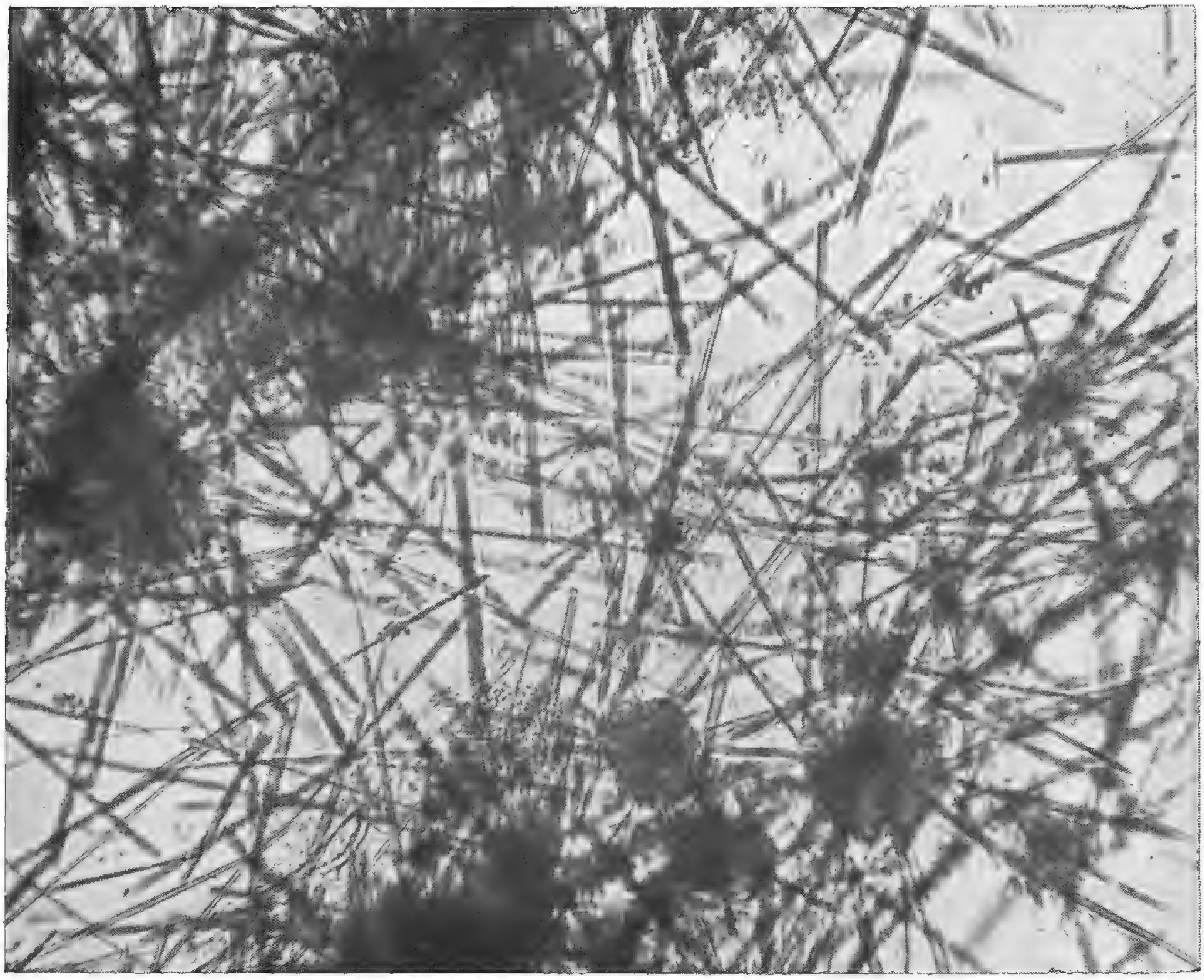


FIG. 3. Microphotograph of a plankton sample with the Acantharian radiolarian *Acanthometra pellucida.* Average weight of each animal was 0.26 micrograms.

Müller (1858) postulated celestite in *Collosphaera,* which is not an Acantharian, in which there is a regular crystal of celestite which Müller was able to study with a goniometer. Bütschli (1906, 1907) really demonstrated that the skeletons were celestite using several methods. Just prior to this, Scheviakov (1902) reported from some of his chemical analyses that the skeletons of these radiolaria were complex silicates. He maintained that point (Scheviakov, 1926). It is easy to account for Scheviakov's interpretation made without x-ray or spectrographic methods. Strontium sulfate is quite insoluble and precipitates from a solution during manipulations in a manner not unlike that of silica. Since a pure sample of radiolaria is not easily obtained from the plankton, the ash will contain certain amounts of iron and aluminum from other sources as reported.

The biochemistry that is associated with this unusual skeletal deposition is still unknown. Although the solubility product of strontium sulfate is small, it is not small enough so that the ionic product of ions of sea water exceeds it. As demonstrated in Figure 4, the solubility goes up as rapidly as the ionic product under conditions of increasing salinity. The solubility product may be exceeded in oceanic conditions only if one of three events takes place. Strontium must be concentrated ten times; sulfate must be concentrated ten times; the total ionic strength must be reduced seven times; or there must be some combination of all three. Lillie described celestite deposition from sea water when the strontium concentration is increased to 0.5M by addition. This corresponds closely to Dinger's solubility product in Figure 4. In the bottle containing the dense plankton sample of Acantharia, the water contained Sr/Ca ratio of 79 atoms/1000 atoms.

The situation is apparently much more complicated than can be explained by solubility products alone because of actions at the colloidal level of integration. The following is a quotation from Morse and Donnay's (1932) discussion of formation of different types of spherules in colloidal solutions:

"An aqueous solution of gelatine containing sulfate ions might be expected to precipitate, say $BaSO_4$ when a solution of $BaCl_2$ is allowed to diffuse into it. This was found not to be the case; the sulfate precipitates only in the presence of a carbonate in the gel (action of a protective colloid)."

The solubility product of strontium carbonate is ten times smaller than the solubility product of strontium sulfate at low ionic strength but the same at high ionic strengths such as in sea water. From the quotation it may be inferred that solubility products within the colloidal medium of the animal are not the same as measured in ordinary solutions. There may be mechanisms for strontium sulfate deposition which involve regular enzyme systems common to other organisms and differing here only in degree.

A curious error has been passed down in some discussions of these radiolaria. Thompson and Robinson (1932) page 175; Sverdrup, Johnson, and Fleming(1942) page 991; Armstrong and Miall (1945). For some reason, although no original worker maintained this composition, these radiolaria were stated to be made of strontium carbonate. Because one or two papers discussed Ancantharian radiolaria collected in the Antarctic, Thompson and Robinson (1932) discussed the comparative solubilities of strontium and calcium carbonate in a paragraph dealing with temperature effects on strontium deposition. The aforementioned discussion seems to have possible validity if $SrSO_4$ is substituted for the erroneously reported $SrCO_3$ and the discussion applied to sulfates. The solubility of strontium sulfate increases with temperature (Wolfman, 1896; Shreve and Watkins, 1939), whereas the solubility of calcium sulfate decreases slightly with increasing temperature (Mellor, 1923 and Shreve and Watkins, 1939) within the oceanic range of temperatures.

Hutchinson (1943) suggests that the Acantharia have few resemblances to the siliceous radiolaria, and should constitute an entirely separate class of Protozoa.

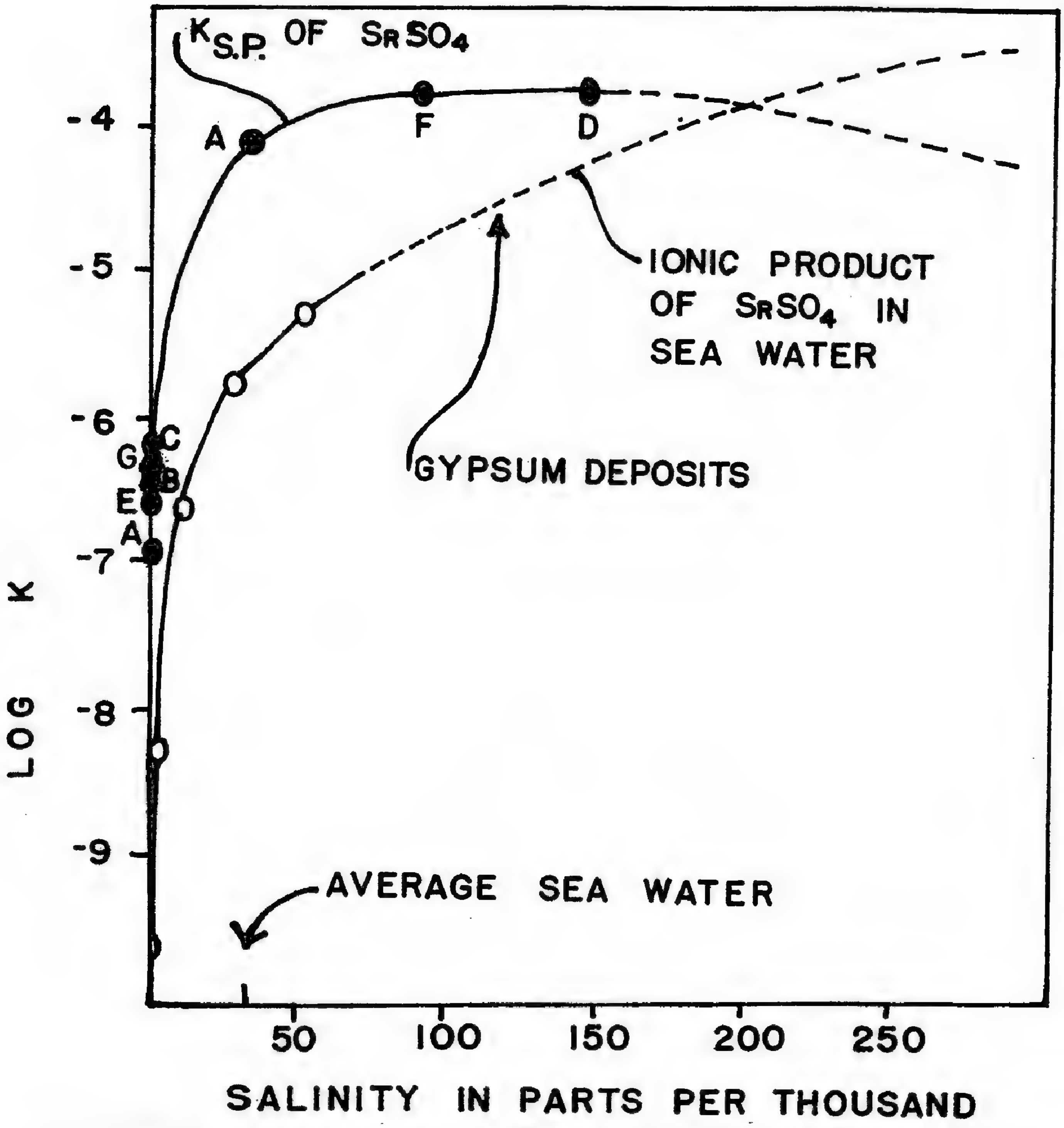


Fig. 4. Solubility relationships of strontium sulfate and salinity of sea water. The logarithm of the solubility product of strontium sulfate as determined by several authors is plotted in the upper line: A, Dinger, 1929; B, Kohlrausch and Rose, 1893; C, Wolfmann, 1896; D, Virck, 1862; E, Holleman from Kraus 1905; F, Fresnius from Kraus, 1905; G, Gallo, 1935. The ionic products of strontium and sulfate in sea water are plotted in the lower line on the assumption of constant ratios of the ions to salinity. Extrapolation of the two lines indicates supersaturation at about 200 parts per thousand. Posnjak (1940) indicated gypsum deposition between 100 and 150 parts per thousand.

4. Strontium Deposition in Sediments

In the preceding discussion a general proportionality between the Sr/Ca ratios of skeletons and aquatic media was concluded. Especially distinct were the differences between marine environments and the fresh waters of humid regions. In some sediments the biological deposition process dominates and thus determines the Sr/Ca ratio of the sediment. In such cases the Sr/Ca ratio in the calcareous parts of sediments is proportional to but less than the Sr/Ca ratio in the water. The Sr/Ca ratio of the water is in turn proportional to the Sr/Ca ratio of the geochemical source regions of the waters (Odum, 1957).

The Sr/Ca ratios of whole sediments, however, depend upon the fine grained, nonbiological, calcareous depositions and upon other mineral components as well as upon the presence of strontium in skeletons. If the Sr/Ca ratio of rocks and sedimentary depositions is to be used to infer the nature of depositional environments, the behavior of the Sr/Ca ratio during various types of sedimentation must be understood. Consider first some of the variations in the Sr/Ca ratio in lake sediments.

STRONTIUM IN THE SEDIMENTS OF OPEN AND CLOSED LAKE BASINS, THE CLIMATIC FACTOR

Hutchinson, Wollack, and Setlow (1943) showed that ratios of strontium, barium, and calcium vary with the type of lake. They indicated that strontium was higher in sediments of closed lakes than in those of open lakes for cases in which the chemical natures of drainages were similar. They also pointed out that the calcium content of closed-lake sediments was in general higher than that in open-lake sediments. Ahrens (1945) noted that of some clays analyzed, saline lacustrine clay from Gilbania, Sinai, had the highest strontium content.

In the present study analyses were made of sediments of open and closed lakes in several kinds of regions as presented in Tables 18 and 20. Re-analyses were made of the Tibet sediments reported in the Hutchinson *et al.* (1943) paper, with rough agreement. The analyses of the acid-extractable fractions of the lake sediments in Figure 5 and Tables 18 and 20 indicate that the closed lakes have a higher strontium content than the open basin lakes. In general the closed basins have a high calcium content although open basins also have a similar wide range of value. Lakes in arid regions may be expected to contain high silt contents because of exposed, unvegetated watersheds. Thus high purity marl sediments in arid areas may be uncommon in spite of high rates of calcium deposition.

In the previous papers (Odum, 1950a, and 1951a, 1957) it is pointed out that for closed lakes in steady state the Sr/Ca ratio of the sediments should be about the same as the ratio in the inflowing tributary waters. In open lakes the rate of calcium deposition in the sediments is less than the rate of calcium inflow. If strontium is excluded relative to calcium during calcareous deposition in such lakes, the Sr/Ca ratio of the sediments will be less than that of the inflowing water. On the other hand in closed lakes the strontium left in the water may be expected to build up to a high value in steady state while in open lakes it flows out. Data indicating operation of the principle are given in Tables 17, 20, and 21 and Figure 5. For example calcareous sediments of Great Salt Lake, Utah (2.08 atoms/1000 atoms), East Twin Lake, Connecticut (0.83 atoms/1000 atoms), and Lake Mendota, Wisconsin (0.52 atoms/1000 atoms) have lower Sr/Ca values than the waters of these lakes (respectively 4.2, 1.32, and 1.77 atoms/1000 atoms) (Odum, 1957) thus substantiating the idea that strontium is excluded during deposition of calcareous sediments.

Turekian (1955) in an interesting note formulated an expression for relating the strontium deposition to the total strontium present during calcium carbonate deposition in closed basins. Reasoning that the Florena Shale in Kansas had properties of a closed basin, he attempted to check the validity of the closed basin ideas with analyses of brachiopods, crinoids, and matrix. He calculated that an observed two-fold range in

TABLE 18

Strontium in the Acid Extracts of Lake Sediments
For strontium analyses of fused residues see Table 21.

	Per Cent Calcium	Sr/Ca Atoms/1000 Atoms
OPEN LAKES		
Wisconsin		
Lake Mary, organic[1]	0.56	2.10
Lake Mendota[1]	8.9	0.52
Clear Lake[1]	0.18	2.92
Trout Lake[1]	0.38	1.07
Tibet		
Yaye Tso[2]	0.54	0.44
Sta-tsa-puk Tso[2]	0.66	2.60
Ororotse Tso[2]	0.62	<1.2
Canada		
Great Slave Lake[3]		
2 miles east of Ethen Island, 15 meters[3]	3.24	3.32
3½ miles west of Pearson Point, 575 meters[3]	3.10	4.82
1 mile north of Pearson Point[3]	2.54	4.07
Resolution Bay, 3.3 meters[3]	1.70	1.53
North Carolina		
University Lake		
Bottom mud 8.3 meters	0.04	4.25
Littoral mud 1.2 meters	0.024	2.40
Singletary Lake, a core		
Organic top mud, Du, 12 ft. below water	1.60	3.06
Gray clay, 13.3 ft. below water	0.22	2.08
Blue clay, 16 ft. below surface of water	0.003	2.10
Organic sand	0.011	0.86
Fibrous littoral peat	0.012	5.8
Connecticut		
Lake Wononskopomac, 60 meters[4]	1.99	0.95
East Twin Lake[4]	11.5	0.83
Bantam Lake, 6.5 meters[4]	0.46	1.65
Black Pond, 6.8 meters[4]	0.88	1.45
Beardsley Park Pond[4]	0.27	2.04
L. Quassipaug	0.2	4.25
Maine		
Caribou Lake, core[4]		
3.15 meters	28.0	1.25
3.50 meters	22.9	1.11
4.0 meters	30.7	1.45
4.23 meters	27.6	1.42
4.5 meters	32.6	1.72
ARID LAKES		
Nevada[5]		
Carson Sink		
SW edge high stage, second Lahonton cycle	0.62	8.17
Carson river delta, second Lahonton cycle	0.54	7.80
Interior, third cycle of Lahonton	0.30	6.45
Interior, second high state	5.4	9.2
Big Washoe Lake, Nevada	1.70	4.89
Tibet[2]		
Mitpal Tso	8.64	1.63
Tso Moriri 50 meters	3.82	3.96
Khyager Tso	13.1	1.62
Tso Dar	10.5	3.13
New Zealand		
Pyramid Valley Swamp[4]	11.3	3.54

[1] Samples from A. Hasler.
[2] Samples from G. E. Hutchinson.
[3] Samples from S. Rawson.
[4] Samples from E. S. Deevey.
[5] Samples from R. Morrison.
[6] See Table 7 for other arid lakes.

TABLE 19

Comparison of Magnesium and Strontium Cycles Relative to Calcium in Two Closed Basins in Steady State: the Great Salt Lake, Utah and the Ocean
Magnesium data are from Eardley (1938). Elemental Ratios by Atoms

	Great Salt Lake		Ocean	
	Mg/Ca Atom/Atom	Sr/Ca Atoms/1000 Atoms	Mg/Ca Atom/Atom	Sr/Ca Atoms/1000 Atoms
Inflow water	0.57	......	0.28	1.30
Water	12.0	4.20	5.2	9.23
Sediments	0.53	1.75	0.27	2.08
Calcareous algae	0.13	... ..	0.23	3.96
Oolite	0.03	4.2	......	9.3
Distribution factor between water and sediment	23	2.3	19	4.6

TABLE 20

Sr/Ca Ratios of Acid Extract of Sediment Cores Suggesting Climatic Change

Depth in Feet	Percent Calcium	Sr/Ca Atoms/1000 Atoms	Possible Climatic Inference
Sediment core from Great Salt Lake, Utah: Specimens from A. J. Eardley			
0–2	4.9	1.75	Arid
2–4	6.7	2.54	Arid
4–6	6.1	1.54	Arid
6–8	5.7	0.90	Wet
14–16	4.2	0.76	Wet
16–18	5.0	0.85	Wet
18–24	3.3	0.93	Wet
Sediments of Pangong Tso, Tibet: 40 meters below water surface; specimens from G. E. Hutchinson			
0.1	7.9	9.65	Arid
0.1–0.3	7.0	4.42	Less Arid

Sr/Ca ratios could not have been achieved in a single environment due to rising strontium contents of the water associated with differential deposition without producing unrealistic chemical conditions for the organisms. Instead of closed basins causing strontium accumulations, he suggested a salinity effect on deposition per se.

The following comment concerns the aforementioned note: (1) This present author's discussions referred to by Turekian on closed basins concerned an open steady state system existing between river inflows and sedimentation rates rather than precipitation in a non steady state in a closed system. Thus the formulation by Turekian refers to temporarily cut-off bodies of marine water without dominant fresh-water inflows but not to closed basins in steady state. Both systems are important paleoecologically although the distinction should be made. (2) Apparently replacement phenomena complicate Turekian's discussion with respect to the Florena Shale data presented. The Sr/Ca ratio of his Crinoids is 0.32 atoms/1000 atoms instead of the much higher, rather uniform value for unreplaced echinoderms of about 3.4 atoms/1000 atoms (Tables 6 and 7). Clarke and Wheeler (1922) analyzed modern and ancient crinoids for magnesium. Finding much less magnesium in the fossils, they also inferred that such material had been altered.

Similarly Turekian's Sr/Ca values of 0.55 atoms/1000 atoms for brachiopods are much lower than values for unreplaced brachiopods of all ages of 1.10–1.81 atoms/1000 atoms. The observed range in Sr/Ca values probably reflects degree of replacement. Turekian in a personal communication indicated agreement with this interpretation. In general semi-closed arms of the sea are likely to produce higher, not lower values of the Sr/Ca ratio in comparison with values in the main sea. Nor are echinoderms expected in environments of extreme salinity. Thus one interprets the Florena shale as partially replaced chemically.

Turekian's formulation is nevertheless important in showing that there will not be very large increases in strontium-calcium ratio in evaporating arms of the sea. Extending interpretation from this premise, one may suggest that any sedimentary Sr/Ca ratio that is much higher than that of modern marine sediments may indicate a closed basin rather than a semi-isolated arm of the sea. Lowenstam, however, in personal communication describes data indicating high Sr/Ca ratios in arms of the sea of high salinity.

Although the Florena Shale data probably don't pertain, there may be a salinity effect on Sr/Ca ratios, nevertheless, due to the decreasing ionic exchange between organisms and media as salinities rise from standard sea water to hypersaline conditions. This effect is discussed in the previous section on biological depositions.

Some examples of Sr/Ca analyses of shells which reflect the arid, high strontium or humid, low strontium character of the basin depositions are as follows: Snails from the shore of the Salton Sea, California in a region geochemically high in strontium had 6.7 atoms/1000 atoms. The mean of 22 aragonite marine mollusks (ocean as a closed basin) was 2.41 atoms/1000 atoms. Snails from Lasal Vieja, Texas (*Balimulus alternatus* collected January 29, 1941 at chlorinity 16,710 ppm by E. S. Deevey) in a sedimentary, arid region had Sr/Ca ratio of 2.31 atoms/1000 atoms. In contrast, the mean of 71 mollusks from open basin lakes was 0.81 atoms/1000 atoms.

Calcareous algae from closed Lake Winnemucca, Nevada had a Sr/Ca ratio 3.53 atoms/1000 atoms. The mean of nine calcite marine calcareous algae was 3.96 atoms/1000 atoms. In contrast, the calcareous algae from open lakes in Michigan had a Sr/Ca ratio 0.52 atoms/1000 atoms.

Some examples of sediments which may indicate changing climates are given in Table 19. For both the Great Salt Lake, Utah and for Pangong Tso, Tibet the more recent sediments show high Sr/Ca ratios correlated with increasing aridity of climate. Estimates by Eardley (1938) suggest a deposition rate in Great Salt Lake of twelve feet per 10,000 years since the last ice age. The Sr/Ca ratio increases in the last seven feet at the time when arid conditions might have been expected. There is a maximum value at the 2–4 foot level that might correspond to a climatic optimum.

STRONTIUM IN SOLUBLE AND INSOLUBLE FRACTIONS OF SEDIMENTS

In order to get direct evidence on the Sr/Ca ratio in various non calcareous components of sediments and soils, the following analytical procedure was used. Acid extracts were analyzed first. Then the residues were fused with sodium carbonate before being extracted a second time for a separate analysis. Whereas the first acid extract includes the strontium and calcium from carbonates, ion exchange binding, and some minor contribution from the silicates or other resistant minerals, the acid extract of the fused residue includes most of the remaining alkaline earths that were part of resistant minerals before fusion.

TABLE 21

Strontium and Calcium Analyses of Soluble and Insoluble Fractions of Argillaceous Materials

	Acid Extract		Na_2CO_3 Fused Residue		Total		
	Per Cent Calcium	Sr/Ca Atoms/ 1000 Atoms Acid Extract	Per Cent Calcium	Sr/Ca Atoms/ 1000 Atoms Na_2CO_3 Fused Residue	Per Cent Calcium	Sr/Ca Atoms/ 1000 Atoms Total	Per Cent Strontium
LAKE SEDIMENTS							
Arid Lakes							
Great Salt Lake, 24"–42"[1]	6.7	2.54	0.20	10.7	6.90	2.77	0.042
Great Salt Lake, 42"–72"[1]	6.1	1.54	0.14	12.2	6.24	1.77	0.024
Klargar Tso, Tibet[2]	13.1	1.62	0.82	7.5	13.92	1.97	0.060
Humid Lakes							
Yaye Tso, Tibet[2]	0.54	0.44	1.58	7.2	2.12	5.48	0.025
Sta-Sta-Puk Tso, Tibet[2]	0.66	2.60	0.76	5.4	1.42	4.10	0.013
Great Slave Lake, Resolution Bay 2 miles west of dock, 3.3 meters[3]	1.70	1.53	0.07	8.3	1.77	1.80	0.007
University Lake, Chapel Hill, N.C., argillatrophic	0.04	4.25	0.05	152.	0.45	20.07	0.020
Singletary Lake, N.C., bottom mud, gyttja	1.62	3.06	0.01	0.6	1.61	4.90	0.017
Singletary Lake, N.C., Gray clay, possibly loess	0.003	2.10	0.002	0.5	0.005	1.46	0.00002
Lake Wononskopomac, Conn.[4]	1.99	0.95	0.32	16.8	2.31	3.14	0.016
Mud Lake, Michigan	1.4	104.	2.09	4.32	......	......	......
SHALES AND MODERN MARINE ARGILLACEOUS SEDIMENTS							
Lower carboniferous, Nova Scotia[5]	12.1	2.66	0.071	13.9	12.17	2.73	0.072
Geneva shale, Moscow, N.Y.[5]	0.6	2.61	0.068	43.3	0.67	6.75	0.010
Burgess Pass, British Columbia, Cambrian[5]	2.6	2.30	0.034	50.0	2.63	2.92	0.017
Athens shale, Bristol, Tenn.[5]	6.3	1.53	0.052	41.6	6.35	1.86	0.026
Marcellus shale, Strandsburg Pennsylvania; Devonian	1.3	1.12	0.115	64.4	1.42	6.26	0.019
Utica slate, Rome, N.Y., Ordovician[5]	0.6	1.74	0.076	57.8	0.68	8.04	0.012
Slate, Millbrook Quadrangle, N.Y., Cambrian[6]	0.16	0.96	......	......	......	......	......
Shale containing Lingula impressions; Conemaugh Formation Maryland; Pennsylvanian[7]	3.8	6.7	0.14	31.2	3.94	7.57	0.066
Shale, Conemaugh Formation[7]	1.9	2.92	......	......	......	......	......
Radiolarite, Borneo, Van Tongeren (1938)	......	......	......	......	......	......	0.01
Radiolarite shale, Oakland, California, Cambrian	0.013	2.10	0.47	16.0	0.48	15.72	0.017
Brachiopod matrix, Ordovician	......	......	0.001	10.5	......	......	......
Modern mud, Buzzards Bay, Mass.[5]	0.71	2.97	......	......	......	......	......
Modern mud, Buzzards Bay, Mass.[5]	0.56	2.91	0.053	18.6	0.61	4.27	0.006
Modern Mud, Hadley Harbor, Mass.[5]	0.20	6.28	......	......	......	......	......
Modern Mud, Hadley Harbor, Mass.[5]	0.47	4.50	0.249	13.5	0.72	7.60	0.012
Black sand, Beaufort, N.C.	0.14	3.32	0.01	......	......	......	......

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[1] Samples from A. J. Eardley.

[2] Samples from G. E. Hutchinson.

[3] Samples from D. S. Rawson.

[4] Samples from E. S. Deevey.

[5] Samples from H. K. Brooks.

[6] Samples from Mrs. A. Knopf.

[7] Samples from C. Waage.

TABLE 22

Strontium and Calcium Analyses of Soluble and Insoluble Components of Soils and Sediments

		Acid Extract		Na_2CO_3 Fusion		Total		
	Number of Analyses	Per Cent Calcium	Sr/Ca Atoms/ 1000 Atoms	Per Cent Calcium	Sr/Ca Atoms/ 1000 Atoms	Per Cent Calcium	Sr/Ca Atoms/ 1000 Atoms	Per Cent Strontium
Mean, humid soils from Table 35	..	0.034	2.12	0.31	10.6	0.34	6.9	0.005
Arid soil from Table 35	..	5.44	1.95	1.72	13.5	7.16	4.8	0.075
Lake sediments								
Humid lakes					(30.4)			
Low calcium	7	0.88	2.12	0.93	.5–152.	1.38	5.9	0.018
High calcium	1	24.10	0.50	4.34	1.5	33.44	0.6	0.044
Arid lakes	3	8.6	1.90	0.38	10.1	9.02	2.2	0.043
Marine muds	2	0.59	3.71	0.15	16.1	0.67	5.9	0.009
Paleozoic shales	7	3.90	2.66	0.08	43.2	3.87	5.2	0.044
Red clay and radiolarite	2	0.16	4.06	0.29	18.6	0.44	13.0	0.013
Glauconite 40° 21′ N. lat.; 71° 00′ W. long.	1	0.95	1.64	0.38	1.04	1.33	1.47	0.004

TABLE 23

Strontium Analyses of Marine Sediments
(Other Data in Tables 21, 24, and 25)

Locality	Depth of Water in Meters	Latitude	Longitude	Age	Depth of Mud in Meters	Per Cent Calcium	Sr/Ca Atoms/ 1000 Atoms
Seamount near Bikini	2360	11° 45′ N	165° 10′ E	....	......	......	2.72
Bermuda[a] Core C-10 #20	1005	32° 19′ N	64° 36′ W	Miocene	Top	35.7	1.53
					1.02	33.4	1.41
					1.70	36.3	1.32
Bermuda[a] Core C-10 #11	2250	32° 15′ N	64° 32′ W	Eocene	Top	33.3	2.14
					1.0	29.2	1.90
					1.70	20.3	2.66
Hudson Canyon[a] Core C-10 #13	3570	38° 22′ N	70° 56′ W	Recent	Top	12.2	2.26
				Pleistocene	3.0	5.7	2.57
Pteropod Ooze[a]	1005	28° 36′ N	77° 10′ W	Pleistocene		32.7	2.38
Aegean Sea[b]							
Phlegers No:							
151–34	104	39° 05′ N	25° 58′ E	....	......	10	2.92
21A·	205	39° 21′ N	26° 03′ E	....	......	21.2	2.59
151–61	462	35° 45′ N	23° 16′ E	....	......	27.0	3.38
Gulf of Mexico[b]							
547	3230	25° 36′ N	89° 21′ W	....	......	31.6	1.66
544	3017	26° 22.5′ N	89° 21′ W	....	......	31.8	1.48
551	3367	24° 59′ N	87° 48′ W	....	......	23	1.47
151	1829	26° 22′ N	92° 54′ W	....	......	33	1.39
44	731	27° 03′ N	93° 52′ W	....	......	32.2	1.55
163	1426	26° 45′ N	94° 55′ W	....	......	17.7	1.70
Glauconite[c]							
Navesink				Cretaceous		0.81	2.00
Monterey Bay, California				Recent?		0.26	3.36
New Jersey				Cretaceous		6.9	2.48

[a] Samples from O. Ericsen.
[b] Samples from F. Phleger.
[c] Samples from H. K. Brooks.

The Sr/Ca ratios from this type of component analysis may be examined for soils and sediments in Tables 21 and 23. It is apparent from these data that the acid fractions are characterized by a low Sr/Ca ratio (0.4–4 atoms/1000 atoms) and the fusion fraction by a high Sr/Ca ratio (0.5 to 17 atoms/1000 atoms). In other words, the components have a pattern similar to that of rocks in general, the insoluble portions generally having a high Sr/Ca ratio and the soluble components a lower ratio. Sediments which have much calcium have low Sr/Ca ratios because the major component is an acid-soluble fraction containing carbonates. When the calcium is low, the fusion component constitutes a relatively larger part, and the Sr/Ca ratio of the whole is higher. Consequently, when the calcium is low, differences between arid and humid lakes may be expected to disappear because the Sr/Ca of the insoluble fraction is a direct function of the type of rock in the drainage rather than the type of outflow.

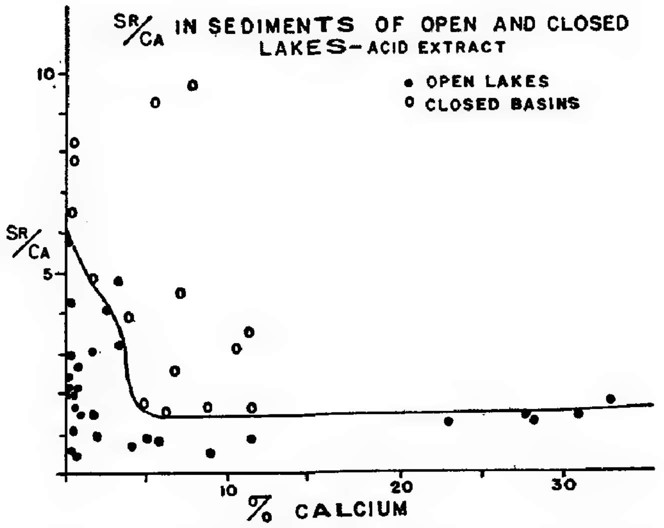
Besides reflecting the per cent of calcium carbonate and the open or closed nature of the basin, the data in Table 18 show some additional regional patterns. The sediments in Nevada lakes in an alkali region have higher Sr/Ca ratios (6 to 9 atoms/1000 atoms) than sediments of the Great Salt Lake (1.6–2 atoms/1000 atoms(in an essentially sedimentary drainage. The Great Slave Lake, Canada and possibly other large lakes because of size have a high ratio of evaporation to inflow, something like that of a closed basin and a fairly high Sr/Ca ratio.

Organic sediments low in calcium in the Wisconsin lakes and Singletary Lake, North Carolina, have moderate Sr/Ca ratios (1–3 atoms/1000 atoms). The Singletary Lake organic sediments have values approximately the same as that of the water (Table 16) suggesting that in organic, low-calcium sediments, the strontium is not excluded during deposition, perhaps because of a non-selective base-exchange binding. The exchange experiment with Singletary Lake peat reported in the section on soils (Table 34) supports this idea. The red clay sediments of University Lake, North Carolina, lack a calcium carbonate component and have a moderately high Sr/Ca ratio characteristic of residual insoluble minerals (2–4 atoms/1000 atoms). Lake Quassipaug, Connecticut, draining crystalline rock is similar. Most anomalous for unknown reasons is the extreme value of the acid soluble fraction of sediments from Mud Lake, Michigan (104 atoms/1000 atoms).

STRONTIUM IN MARINE SEDIMENTS

With respect to the overall behavior of the Sr/Ca ratio, the ocean is a closed basin. Because of these closed characteristics, and the high Sr/Ca ratio of sea water, marine calcareous sediments have a higher Sr/Ca ratio than the calcareous sediments of the open fresh waters measured. However, because of the size and diversity of the ocean there is a great range in the Sr/Ca ratio as indicated in the data of Tables 19–23.

The Sr/Ca ratio varies with depth in part because of the restriction of calcareous deposits to the shallower waters. In the deeps or locally where silt deposition is large, the Sr/Ca ratio is due principally to the acid insoluble fractions. Elsewhere in shallower, carbonate-rich sediments where no direct chemical precipitation occurs, the Sr/Ca ratio is determined by the taxonomic composition of the carbonate precipitating organisms, which are locally dominant. Consequently, in marine sediments as in lake sediments there is an inverse pattern of Sr/Ca ratio and calcium composition as shown in Figures 5, 6, and 7. Apparently as the calcium content diminishes, the Sr/Ca ratio approaches that characteristic of the acid insoluble fraction. As the calcium content increases, the Sr/Ca ratio approaches that of the carbonates present. Calcareous oozes from medium depths have lower Sr/Ca values than more littoral carbonate sediments (Table 24)



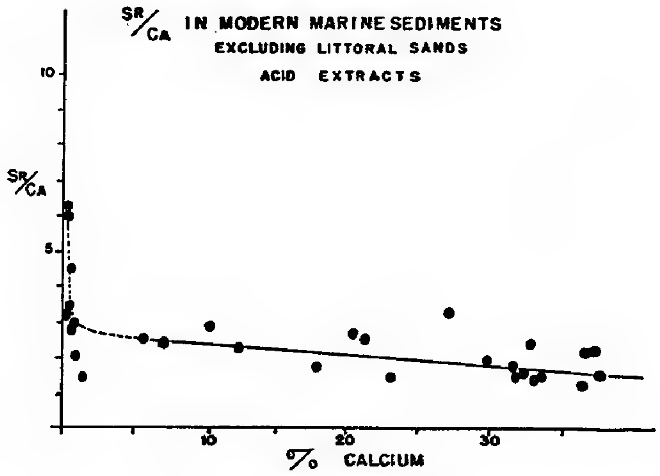


FIG. 5. Sr/Ca ratios of the acid extracts of lake sediments plotted as a function of the calcium content. A line is drawn almost separating basins without appreciable outflow (closed basins) from basins in humid regions which overflow (open lakes).

FIG. 6. Sr/Ca ratios of acid extracts of marine sediments as a function of the calcium content. Littoral sands have been omitted as unrepresentative of major sedimentation for purposes of the discussion in the text. A line is drawn to indicate the hyperbolic shape of the distribution.

partly because of the low Sr/Ca ratios of pelagic foraminifera. The highest Sr/Ca values are contained in coral reefs or areas of suspected direct chemical precipitation. The littoral deposits are subject to great variation because of the differences in the taxonomic components. The great variation in Sr/Ca ratio in the littoral sands reported in Table 25 is an example.

The data in Tables 20 and 21 indicate that the high Sr/Ca content of marine sediments is in the acid-insoluble fraction. This suggests that the strontium is contained in the more resistant silicates. Whether some of these are formed diagenetically or not is uncertain. Similar patterns are found in soils and lake sediments. Accounting for the relatively high Sr/Ca ratios observed in the argillaceous sediments and acid-insoluble sedimentary components is more difficult than accounting for the strontium content in calcareous components. Noll (1934) has interpreted some of the high Sr/Ca values of clay materials as indicating a differential base exchange uptake of strontium relative to calcium. A base exchange experiment on a marine sediment (Table 34) does not support this hypothesis.

Turekian and Kulp (1956) found higher values for Sr/Ca ratio in shales with low calcium content that they called "pure shale." They interpreted this as due to binding of strontium more than calcium in base exchange. The component analyses, however, suggest that the strontium is in some more firmly bound constituent which requires sodium carbonate for release.

Because of the deposition of potassium in clay minerals such as glauconite forming on the ocean floor it might be suggested that some strontium would enter the sediments in this form because of the similarity of ionic radii to that of potassium. However, neither the acid extract (1.64 atoms/1000 atoms) nor the analysis of the residue of glauconite (1.04 atoms/1000 atoms) showed a high Sr/Ca ratio. Cormier *et al.* (1956) found a wide strontium variation in some ancient glauconites (10–116 ppm).

In obtaining averages for geochemical calculations of strontium in sediments, Figure 6 is used. To find the Sr/Ca for the average red clay, the intersection is found between the average of many red clays of 1.4 per cent calcium on the diagram and the curve through the plotted points. The result is a lower Sr/Ca value (4 to 5 atoms/1000 atoms) than the value that would be obtained from the few analyses of strontium in red clay

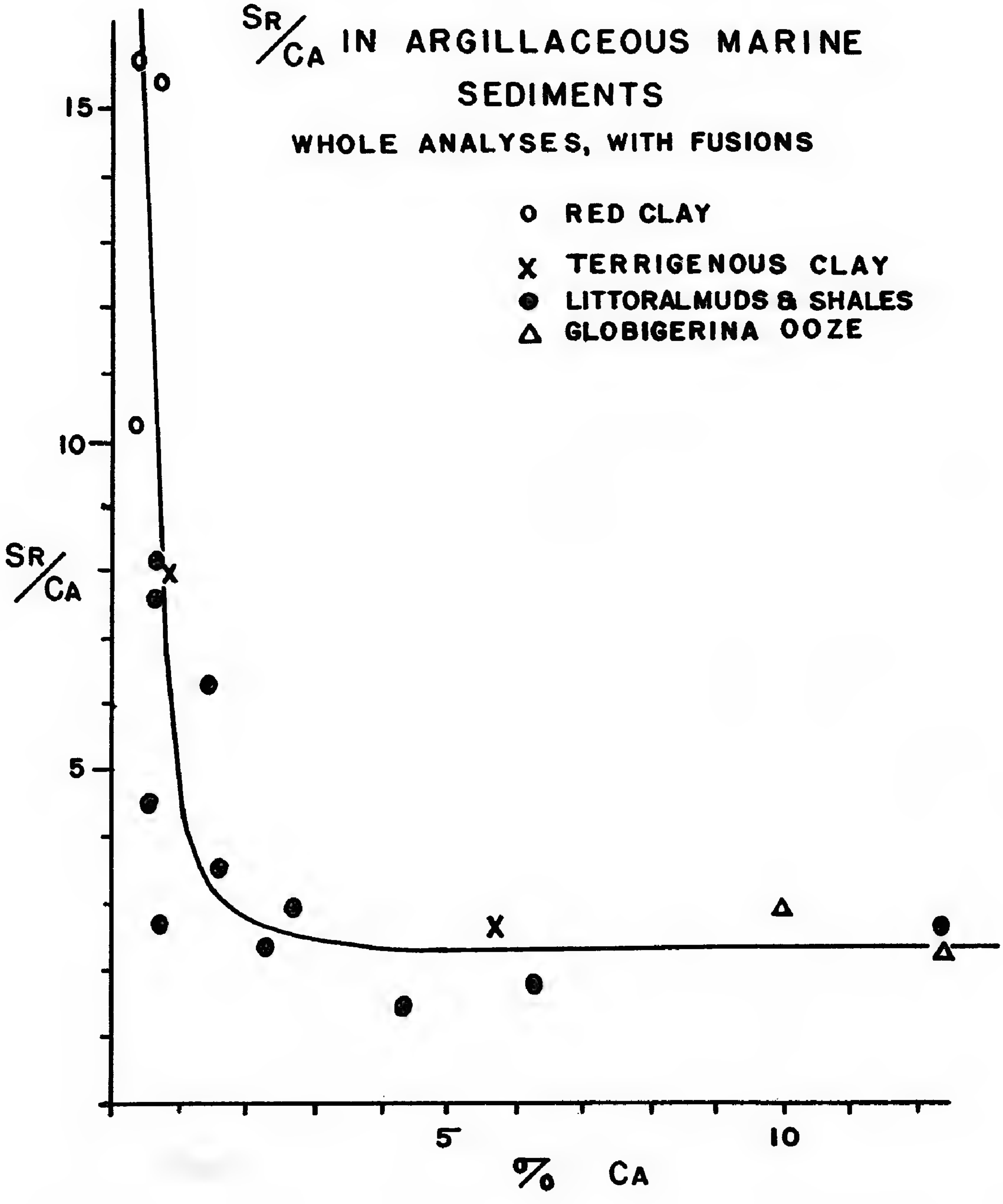


Fig. 7. Sr/Ca ratio of argillaceous (low in carbonate) marine sediments. In contrast to Figures 5 and 6, these data include the alkaline earth content both from the acid extracts and from sodium carbonate fusions of the extracted residues. A lines is drawn suggesting a hyperbolic relationship.

available (13 atoms/1000 atoms). This is because the samples averaged contained less calcium than most other red clays. Hevesy and Würstlin (1934) found 0.003 and 0.013% strontium in two red clay samples which compares well with 0.013% (Table 22).

In Table 24 and in other analyses reported in the review by Revelle and Emery (1951), the Sr/Ca ratio of barite nodules is very high (70 atoms/1000 atoms). The above authors suggest that the high strontium content indicates origin from hot solutions

TABLE 24

Strontium Analyses in Comparative Marine Sediments
For other data see Tables 23 and 25

	Number of Cases	Per Cent Calcium	Sr/Ca Atoms/1000 Atoms
Littoral calcareous sand, Table 25	10	......	5.21
Pteropod ooze[1]	1	32.7	2.38
Foraminiferal ooze			
Surface to 1000 meters	4	22.6	2.61
1000m to 3400 meters	8	30.3	1.49
Sample with coral fragments	1		7.0
Phosphate nodule[2]	1	10.9	3.47
Terriginous mud	2	0.66	5.9
Littoral new analyses, acid extract only	5	0.4	4.00
Composite of 52 terrigenous clays (Steiger, Hillebrand and Sullivan in Clarke, 1924)		0.82	7.94
Glauconite sediments[3]	4	2.1	2.33
Radiolarian shale, Cambrian[4]	1	0.48	15.7
Red Clay[1]	1	0.4	10.2
Composite of 51 (Steiger, Hillebrand and Sullivan in Clarke, 1924)	1	0.78	15.4
Barite nodule[5]	1	1.8	69.9
Manganese nodule (Gibson, 1891 in Clarke, 1924)	1	5.5	10.9

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[1] Samples from O. Ericsen.
[2] Samples from S. Hendricks.
[3] Samples from H. K. Brooks.
[4] Samples from Yale Peabody Museum.
[5] Samples from K. Emery.

ascending along a fault scarp in contact with the sea bottom. The high Sr/Ca ratio often found in mineralized waters supports this idea.

Another aspect of marine sedimentation is the deposition of strontium sulfate in radiolarian skeletons (Odum 1951b). Samoilov (1917) thought that biological deposition of strontium in skeletons of Acantharian radiolaria may have been important in the past. Noll (1934) found that there was no evidence for appreciable radiolarian-deposited celestite in the past. The contribution of celestite is very small, although it has a high Sr/Ca ratio. It is only when the carbonate contribution is very small that a small strontium sulfate component might be noticed. In the analyses of red clays reported in Table 20 and Figure 5, the Sr/Ca ratio is high (15 atoms/1000 atoms) but not much higher than in similar components of fresh-water sediments and soils. Celestite deposition cannot therefore be large. $SrSO_4$ is soluble in sea water, so that celestite is not expected in areas in contact with the ocean surface at ordinary salinity. Celestite in the Acantharia is discussed in the section on biological deposition of strontium.

STRONTIUM IN PHOSPHATE DEPOSITS

An interesting part of the strontium cycle involves the deposition of strontium in sedimentary phosphate deposits. Noll (1934) found a moderately high absolute concentration of strontium in a phosphate deposit, and a number of other scattered quantitative analyses of phosphates for strontium were tabulated by Gray (1943). Young (1935) analyzed strontium in many phosphatic materials being used for fertilizer. The widespread distribution of strontium was confirmed by the qualitative analyses of Jolibois and Hebert (1946). In Table 4 are new and old analyses which indicate that the Sr/Ca ratios in phosphate deposits have a range of values (0.5 to 8.0 atoms/1000 atoms)

Table 25

Strontium Analyses of Limestones, Limestone Precursors, Marine and Continental Sediments

	Number Cases	Sr/Ca Atoms/1000 Atoms
Diverse littoral calcareous sands		
St. John, Antiqua[1]	1	7.33
Eastern United States	1	0.57
Santa Catalina Island, California[1]	1	1.88
Gulf of Oran[1]	1	1.92
Red Sea[1]	1	6.85
Branford, Connecticut[1]	1	2.48
Bikini coral sand[3]	1	10.89
Bikini *Halimeda* sand[3]	1	13.00
Rongelap atoll[3]	1	3.65
Rongerick atoll[3]	1	3.54
Bimini, Bahamas,[2] thin section showed consolidated forams	1	9.45
Bahama I, Bahamas	1	8.00
Calcareous sands, mean of above:	11	5.59
Skeletal components of limestones; average	5	4.73
Coral reef (including dolomitized parts)	25	5.61
Miocene fossiliferous marl	1	2.78
Marine chalks	3	1.49
Precambrian limestones	5	0.97
Silurian-Pennsylvanian fossiliferous	8	0.92
Cambrian-Ordivician, not fossiliferous	10	0.72
Cambrian and Ordivician dolomites	13	0.40
Limestones with some celestite, data of Stout (1941); overall value for deposit	196	3.13
Limestone of Carboniferous evaporate deposit, with celestite, data of Vinogradov and Borovik-Romanova (1945)	164	6.16
Estimate of Sr/Ca of terrestrial limestones for geochemical calculations, mean of above:	....	2.68
Estimate of Sr/Ca of observed surface limestones representing end product of diagenesis	...	1.21
Consolidated oolite, Key West	...	10.0
Consolidated oolite, Bimini[4]	....	9.30
Limestone crust attached to above oolite sample, Bimini[4]	....	0.90
Drewite, Bahamas[4]	....	10.5

[1] Samples from Peabody Museum.
[2] Samples from F. H. Wood.
[3] Samples from J. Tracey.
[4] Samples from Louis S. Kornicker.

similar to that in other sediments and limestones. Because of the calcareous nature of phosphate deposits the absolute quantity of strontium is considerable even though the Sr/Ca ratio is only moderate. Consider, now, the data in Table 4 for evidence as to the factors regulating the Sr/Ca ratio in phosphates.

Igneous apatites, as discussed in the section on strontium in minerals (Table 4), have a strontium content that was determined by the amount of strontium present at time of deposition. Thus as shown in Table 1, Russian apatites and Khibiny strontium apatite (Fersman, 1929) forming in the final stages of a fractional crystallization process contain a very high Sr/Ca ratio (30 atoms/1000 atoms). Similarly phosphates in Leucite (Noll, 1934) and from a Uganda volcanic rim have a relatively high Sr/Ca ratio. In contrast, Quebec apatite associated with contact metamorphism, Brazilian apatite, and appatites reported by Noll in gabbro and ilmenite, deep basic rocks formed early in fractional crystallization processes, have low Sr/Ca ratios (0.2—0.6 atoms/1000 atoms). Goldschmidt (1954) describes the wide range of strontium in apatites from different localities. The data on the strontium content of the igneous crystals indicates a similarity between strontium occlusion in apatites and carbonates regarding range and magnitude.

Sedimentary phosphate deposits are derived in two principal ways, from guano deposits and from concentration of sedimentary phosphates by weathering processes. As discussed by Hutchinson (1950) a series of climatically controlled diagenic processes beginning with guano deposition by birds is responsible for many of the insular phosphate deposits of the world. Of biogeochemical interest is the metabolism of strontium during these processes. Fresh guano (Table 4) although possessing a considerable calcium content has a low Sr/Ca ratio (1.2 atoms/1000 atoms). This is apparently because the calcium in the bird deposits is derived from fish bones. As shown in the section on biological deposition of strontium, bone deposition in fishes excludes strontium so that the Sr/Ca ratio is quite low (1.3 to 3 atoms/1000 atoms). Thus phosphates derived from piscivorous bird guano may be expected to have a low Sr/Ca ratio.

In the following section on replacement it is postulated that waters percolating through calcareous formations pick up the strontium faster than calcium. If this is so diagenetic processes may be expected to lower the Sr/Ca ratio even further. The solubility product data (Joseph, 1939) indicate that calcium oxalate (S.P. 1.78 x 10^{-9}) is more insoluble than strontium oxalate (S.P. 56.1 x 10^{-9}). Thus, natural chromatographic processes involving oxalates found in phosphate deposits should lower the Sr/Ca ratio. Rogers (1924) studied the chemistry of fossil vertebrate bones concluding that the replacement of the alkaline earth elements was common and deceiving. He thought phosphate ions less mobile than the cations.

Unexpectedly, however, the analyses given in Table 4 show many guano-derived insular phosphates with higher Sr/Ca ratios than might be expected from a fish origin. It is postulated that these phosphates have been derived not only from the guano but from coral rocks which have very high Sr/Ca ratios (10.0 atoms/1000 atoms).

In order to test the correlation of strontium of insular phosphates with carbonate association, qualitative estimates were made of the fizzing (effervescence) of 0.2 gm samples of the insular phosphates dropped into 20% hydrochloric acid in crucibles. The Sr/Ca ratio of 11 samples which showed appreciable effervescence was between 1.9 and 8.0 (mean, 4.3) atoms/1000 atoms. The Sr/Ca ratio of 9 samples which did not show fizzing was between 0.5 and 2.7 (mean, 1.2) atoms/1000 atoms. Apparently, therefore, the strontium content of phosphate deposits may be dependent in large part on the Sr/Ca ratio of associated carbonate rocks.

Because the Sr/Ca ratio in fresh bones, teeth, and phosphatic brachiopods is low (1 to 3.5 atoms/1000 atoms), phosphate deposits formed initially from these skeletons may be expected to be lower in ratio than those insular deposits associated with coral. The fairly low Sr/Ca ratios between 0.82 and 5.69 for continental deposits (Table 4) are in fair agreement with the supposition.

The Florida, Tennessee and Idaho phosphate deposits have Sr/Ca ratios which if anything are even lower than the unmodified bones and teeth indicating that the phosphate concentration process probably selectively removes strontium. Several of the insular deposits show evidence of lowering of Sr/Ca due to replacement such as Nauru, Christmas, Ocean, and Angaur deposits described as being located above dolomitized and replaced limestones.

The strange marine phosphatic nodules known in many parts of the world studied by Dietz, Emery, and Shepard (1942) and Emery and Dietz (1950) have apparently been deposited or involved reworking in contact with sea water. As shown by the analysis in Table 28 the deposition process lowers the Sr/Ca ratio in the nodule (3.47 atoms/1000 atoms, Table 5), in comparison to that in the sea water (9 atoms/1000 atoms). The strontium seems to be selectively excluded just as in organic deposition of bones and phosphatic shells in marine organisms. When Young (1935) analyzed phosphatic fertilizer materials, he found low values indicating possibly that the process of making superphosphate excluded strontium.

It is postulated in the following section on replacement that percolating waters tend to lower the Sr/Ca ratio in carbonate and phosphate rocks. On the other hand the fluorine content of such reworked deposits has been shown to increase with time where terrestrial deposits are being derived from concentration of sediments (Oakley and Hoskins, 1950; Clarke, 1924; Marshall, Jacob, and Reynolds, 1932). Thus if replacement lowers the strontium content, the presence of strontium must be inversely correlated with that of fluorine.

The strontium data in Table 4 were used to test the hypothesis. Fluorine analyses are available for many of the samples analyzed in Table 4 from previous publications (Reynolds, Jacob, and Hill, 1929; Marshall, Jacob and Reynolds, 1932; Jacob, Hill, Marshall and Reynolds, 1933). Of deposits analyzed in Table 4 fluorine analyses were readily available for 15 continental deposits and 8 insular deposits. That the fluorine in the continental deposits was high (3.4%; 1.7 to 4.2%); whereas that in the insular deposits was lower (1.5%; 0.4 to 2.3%), is support for the hypothesis that the Sr/Ca ratio is lowered in replacement processes. There is apparently a very distinctive separation of phosphate deposits into two classes: (1) continental deposits, low in strontium, high in fluorine, and probably of replacement origin; (2) insular deposits, low in fluorine, of guano origin, and with a wide Sr/Ca ratio range depending on carbonate admixture. The igneous and metamorphic phosphates can have both high strontium and high fluorine content.

Hodge, Gavett, Thomas (1946) studied the adsorption of strontium on phosphates. Strontium was adsorbed most on bone, next on apatite and dentine and least on enamel possibly because of particle sizes. Strontium exchanged faster than fluorine and sodium but slower than phosphate.

STRONTIUM IN THE DIRECT DEPOSITION OF CALCIUM CARBONATE FROM WATERS

In discussion on the strontium content of lake sediments, in marine oozes, and in loose assemblages of skeletons, emphasis was laid on the lower Sr/Ca ratio usually found relative to that in the aquatic medium from which the materials sedimented. However, in a few situations some very high Sr/Ca ratios were observed which suggested that in some sedimentary processes Sr/Ca values equal to or greater than those of the aquatic medium could occur by inorganic processes alone. Abundant evidence is available concerning the chemical precipitation of carbonates to indicate that if the solubility products are much exceeded, and if the solutions are not allowed to exchange with large resevoirs of media so that precipitation takes place in enclosed areas, Sr/Ca ratios equal to those of the medium occur. For example adding sodium carbonate to sea water (Sr/Ca 9.0 atoms/1000 atoms) at various rates in 5 cases produced calcium carbonate precipitates with Sr/Ca ratio varying from 4.9 atoms/1000 atoms to 13.3 atoms/1000 atoms. Many similar data are given by Zeller and Wray (1956), and Wattenberg and Timmermann (1938) found that the solubility product or carbonate in sea water was about the same for both strontium and calcium (5×10^{-7}) whereas in distilled water the solubility product of strontium carbonate (0.3×10^{-9}) was much smaller than that of calcium carbonate (5×10^{-9}). Thus direct precipitation in low salinity water is even more likely to deposit high Sr/Ca ratios than in salt water.

It is not easy to prove the applicability of a principle of high Sr/Ca ratio in rapid or restricted inorganic precipitation because the occurrence of direct precipitation is itself in dispute especially in regard to deposition directely from the sea. Direct deposition has been proposed for several types of materials in the warm tropical waters of the Bahamas and similar marine environments. Aragonitic needles termed Drewite have controversially been suggested as one form of direct deposition, but Lowenstam (1955) finds similar needles in the tissues of marine algae and suggests that this may be the source of Drewite. The conditions which produce oolite have not been uniformly agreed upon although they can be readily produced for many kinds of chemical precipitation in the laboratory if the right kind of organic matter is present (Morse and Donnay, 1932). There is little doubt that many oolites involve direct inorganic precipitation although evidence to show exactly what conditions produce the deposition in the Bahamas has been slow to appear. Recent experiments of Monaghan and Lytle (1956) suggest that where solubility products are much exceeded as in rapid deposition, spherulitic precipitation occurs whereas slower precipitation produces needles.

The Sr/Ca ratio casts some light on these issues, although the situation is clouded somewhat by the associated presence of fragments of those organisms whose skeletons have Sr/Ca ratios as high as the sea such as aragonite reef corals (9 to 12 atoms/1000 atoms) and aragonite green algae (10 to 13 atoms/1000 atoms). The Sr/Ca ratio is very high (9 atoms/1000 atoms or greater) in three situations where direct precipitation is suspected by some workers in the Bahamas, Key West, and fossiliferous deposits of Miami: (1) Unconsolidated and consolidated oolite (9 atoms/1000 atoms), (2) Drewite, 9.3 atoms/1000 atoms, (3) consolidated and cemented rocks whose fragments are made up of taxonomic components not originally high in Sr/Ca ratio like the foraminifera (sample from Bimini, 9.5 atoms/1000 atoms, see Table 10). The high Sr/Ca ratio of Drewite is similar to the high ratio in calcareous green algae but also similar to the Sr/Ca ratios possibly achieved in direct deposition from sea water. The Sr/Ca ratio of oolite found from the Great Salt Lake (4.23 atoms/1000 atoms) is the same as that of the water (4.20 atoms/1000 atoms). High Sr/Ca ratios also occur in calcite and aragonite pisolites from springs (Table 5).A Sr/Ca ratio of 5.2 atoms/1000 atoms was found in pisolite from Karsbad, Bohemia where Clarke (1924) reported a ratio in the water of 2.7 atoms/1000 atoms.

The formation of beachrock by cementation of unknown origin (Emery and Cox, 1956) is another peculiar case. Cloud's suggestion of blue green algae in the upper zones causing solution and reprecipitation due to large pH changes diurnally associated with metabolism is a most interesting suggestion. In fact the high Sr/Ca ratio of all reef corals and green algae may be due to the same phenomenon since these skeleton building colonies have symbiotic zooxanthellae and green algae in surprisingly large biomass (Odum and Odum, 1955). Thus the high Sr/Ca ratios of cemented sands, calcareous algae, and reef corals may be due to similar phenomenon associated with algae. Emery and Cox's objection to blue green algae for cementation of beach rock (1956) was that deep layers could not be thus cemented. This is not an objection if the rock is laid down from the top in concentric layers.

If rapid deposition is a requirement for oolite deposition, the very great diurnal activity of photosynthesis in turtle grass and reef environments (Odum, 1957) may be responsible. Thus high Sr/Ca ratios, greater than 9 atoms/1000 atoms, may be a paleoecological indication of algae photosynthesis either within or near the depositional substrate.

One is certainly tempted to believe that Sr/Ca analyses along with thin section examination, can be used to indicate environments of direct chemical deposition of calcium carbonate in the sea. Certainly there is a great difference between Sr/Ca ratios of littoral tropical sands, oolites, beach rocks on the one hand and other marine calcareous sediments on the other. Nothing could be more different than the Sr/Ca ratio of 10 atoms/1000 atoms of such depositions and the non fossiliferous Cambrian and Precambrian limestones of New York with Sr/Ca ratio closer to 0.8 atoms/1000 atoms. This situation leads one to the discussion of replacement phenomena and a controversy over the ancient sea.

STRONTIUM IN ORGANIC RESIDUES, COAL AND OIL

Somewhat related to strontium metabolism during consolidation of sediments is the problem of the strontium content in organic residues. At the present state of our knowledge, the strontium contents of both coal and oil are known to vary greatly as indicated in the collection of a few new analyses and reports from the literature in Table 26. It is

TABLE 26

Sr/Ca Ratio in Plants, Coal, and Oil

Source	Strontium Per Cent of Ash	Sr/Ca Atoms/1000 Atoms
COAL		
Pennsylvanian samples[a]		
Cannel coal, Lincoln Co., Missouri	0.014	10.9
Bituminous coal, Bates Co., Missouri	0.013	9.7
Anthracite, Mahoney Basin	0.006	8.8
Anthracite, Shenandoah	0.03	88.0
Nitrate method (Thilo, 1934)	0.14	18.0
X-ray spectra (Noll, 1934)		
Niederschleisen-coal	0.02	0.5
Ruhr—anthracite	0.01	2.0
(López de Azcona and Pulg, 1947)	0.001	......
N. Wales (Reynolds, 1948)	0.01–0.1	......
Coal ashes of New Zealand (Rafter, 1945)		
From Mangapehi	1.3	......
From Waikato	0.3	......
PLANTS AND PEAT IN SINGLETARY LAKE, N.C.		
Modern Fibrous Peat	0.047	5.8
Mean of 10 analyses of the plants growing on the peat	0.185	4.94
OIL		
Crude petroleum, Bear Oil Co., Leduc, British Columbia, oil pool above coral reef	0.005	6.5
Oil ashes, Katchenkov (1948)		
Devonian	0.03	......
Carboniferous	0.09	......
Jurassic	0.18	......
Tertiary samples	0.2	......
	0.18	......
	0.5	......
	0.3	......
	0.2	......

[a] Samples from A. Bateman.

possible that these values are a function of the materials from which they are derived and might be used to indicate the origin of petroleum or coal. However, there is not yet enough data to make a coherent pattern. It is interesting that the Leduc oil field sample of petroleum has a Sr/Ca ratio similar to that of a coral reef since the oil pool is in a cap at the top of the reef.

The very high strontium contents in some of the reported coals are not understandable at present since modern vegetation as studied so far does not concentrate strontium many times relative to soil solutions. The Sr/Ca ratio of peat from Singletary Lake N. C. (5.8 atoms/1000 atoms), suggest that peat formation process does not greatly modify the Sr/Ca of the contributing plants (4.9 atoms/1000 atoms).

The report by Katchenkov (1948) of a variation in geologic time in the strontium content of petroleum ashes is most interesting if substantiated. The now controversial evidence presented on strontium in geological time (Odum, 1950b, 1951a; Kulp, Turekian, and Boyd, 1952) suggests a constancy of strontium in the ocean so that the differences in the oil ashes if verified possibly represent some differences in the types of sources for oil with time. Further study might lead to an understanding of what taxonomic remains were the source of oil and to the time of origin of plants such as brown algae which have distinctively high Sr/Ca ratios (40 atoms/1000 atoms.

5. Strontium in Limestones and Fossils; Replacement, Recrystallization and Weathering

Data on strontium in limestones and limestone precursors are now fairly extensive with analyses reported by Engelback (1862), Noll (1934), Stout (1941), Sahama (1945b), Vinogradov and Borovik-Romanova (1945), especially Kulp, Turekian, and Boyd (1952), Chilingar (1956), and others. Some additional analyses are given in Tables 25, 27, 28 and 29. The Sr/Ca ratios of most but not all limestones analyzed (0.1 to 2.0 atoms/1000 atoms) are lower than those of unconsolidated sediments (1.3 to 10 atoms/1000 atoms). Some of the older limestones are especially low, 0.72 atoms/1000 atoms. From these low values an issue is immediately apparent. Either strontium has been lost in the process of consolidation or the precursors of the ancient limestones had lower Sr/Ca ratios at the time of initial deposition.

STRONTIUM IN REPLACEMENT PROCESSES DURING LIMESTONE FORMATION

Noll (1934) summarized much of the evidence bearing on diagenetic processes with respect to strontium and concluded that strontium was enriched in percolating waters and depleted in carbonate components of sediments. It was concluded that celestite was one outcome of this process when the waters with high strontium came in contact with sulfate either in solution or as a mineral. He indicated that particularly in the recrystallization from aragonite to calcite strontium would be released. The evidence from pseudomorphs has shown that because the solubility product of strontium carbonate in salt water (S.P. 5×10^{-7}) is smaller than that of strontium sulfate (S.P. 10^{-5}), strontianite will replace celestite and celestite will replace gypsum (Mugge, 1899). Dinger (1929) showed how celestite should replace gypsum because of solubilities. It has been

TABLE 27

Strontium in Limestones

	Per Cent Calcium	Sr/Ca Atoms/1000 Atoms
Cambrian and Ordovician Series from New York[1]		
Lower Cambrian, Dolomite	21.5	0.23
Sample 1	19.5	0.32
Sample 2	19.0	0.35
Sample 3	18.9	0.31
Sample 4	19.4	0.43
Crusts resembling algae, quartz dolomite	19.1	0.29
Dolomite	18.0	0.39
Ridges resembling algae, dolomite	18.8	0.19
Upper Cambrian		
Dolomite	16.4	0.57
Dolomite	7.3	1.28
Dolomite	21.7	0.39
Limestone	14.1	0.59
Alga, Pine Plains High School, New York		
Outside material	17.7	0.31
Center of alga	16.8	0.41
Cryptozoan	36.4	0.57
Cryptozoan matrix	23.7	0.72
Ordovician Limestones		
Sample 1	34.2	0.76
Sample 2	17.3	1.10
Sample 3	15.0	0.42
Sample 4	27.3	1.20
Sample 5	24.3	0.57
Ordovician, Stockbridge Marble, Connecticut		
Canaan	......	0.27
Lake Wononskopomac	......	0.19
Ordovician Islands, Versaille, Indiana, replaced coral[4]	......	0.55
Cambrian, Pleospongiae limestone, Newfoundland		
Sample 1	......	0.34
Sample 2	......	0.34
Ordovician, fossiliferous limestone, Devon Park, Kentucky[4]	......	1.23
Silurian, fossiliferous limestone, Rosendale, New York	......	1.43
Precambrian Limestones		
Proterozoic, Green Head formation[3]	23.0	0.50
Hastings Transition to Grenville, Ontario[3]	36.5	2.00
Grenville, Ontario[3]	29.8	0.22
Grenville, Ontario[3]	30.2	0.29
Belt Series, Montana, Proterozoic, with *Cooperia*	33.7	1.85
Algal structure, Beltian, Late Proterozoic, Wyoming[3]	......	0.47
Algal structure, Proterozoic, Wyoming[3]	......	0.36
Eozoan canadense[2]	......	0.43
Miscellaneous		
Calcareous sinter forming beneath moss[6]		
Margara cuesta, talus, Lockport Dolomite, Rattlesnake Point, Milton, Ontario	38.0	0.18

[1] Samples from Mrs. A. Knopf.
[2] Samples from M. A. Fritz.
[3] Samples from B. F. Howell.
[4] Samples from Willard Hartmann.
[5] Samples from Yale Peabody Museum.
[6] Sample from F. P. Ide.

pointed out in the previous paper on natural waters (Odum, 1957) that mineralized waters are often characterized by a high Sr/Ca ratio.

It had been suggested many times before (Andree, 1914, Hill, 1916; Dinger, 1929) that the celestite associated with dolomite deposits contains the strontium that was released from limestone in the formation of dolomite. Conversely, it had been suggested that if the dolomitization had occurred directly in a high salinity water, the strontium not included was crystallized separately as celestite.

TABLE 28

Strontium in Comparative Dolomite Types

	Celestite	Number of Analyses	Sr/Ca Atoms/1000 Atoms
Funa-Futi Atoll, 624–935 feet in boring	not reported	5	0.82
Cambrian, New York	apparently none	13	0.40
Florida, Tertiary	none	3	0.54
Paleozoic, Ohio, data of Stout (1941); two natural groups:			
Very low strontium	none	176	0.20
Very high strontium	much present	20	29.15
Carboniferous dolomite-evaporate from borings. Data of Vinogradov and Borovick-Romanova (1945).	much present		
Component deposits:			
Limestone		13	1.96
Anhydrite		7	3.60
Gypsum		8	8.04
Dolomite		36	11.44
Weighted mean for total deposit		64	6.16
Permian, celestite-bearing dolomitic anhydrites	0.1–0.2%	....	3.0

Y. Tsuchiya (1944, 1948) reported strontium analyses of fresh corals in comparison to the exposed coral skeletons on a beach. Using a chemical separation procedure, he indicated that the fresh corals had a higher strontium content than the leached corals. To check this work an analysis of variance of the data was performed. The differences were not found to be significant. Also, the values for corals given are twice those of other workers (Chow and Thompson, 1955; Odum, 1950b, Table 6; Bowen, 1956).

Kulp, Turekian, and Boyd (1952) followed by Chilingar (1956) analyzed several hundred limestones and fossils with an arc spectrographic method with general agreement with the present work (Odum, 1950b) with respect to (1) a generally low Sr/Ca ratio (0.76 atoms/1000 atoms) for Paleozoic limestones, (2) similar values in cold and warm environments for two modern animal skeletons, and (3) a higher Sr/Ca ratio in fossils than in fossil matrices.

There is some suggestion that these are spectrographic analyses for those materials that were not fairly pure limestones may not be equally accurate. Calcium carbonate standards were used. Whereas dolomites analyzed by the present author were especially low in Sr/Ca ratio, the values reported by Kulp and associates were correlated somewhat with magnesium. Chilingar found no relationship between strontium and magnesium. In the present study all limestones and dolomites were reprecipitated with oxalate and ashed to carbonate in an effort to avoid possible interference from contained iron, aluminum, and magnesium. Whether the values for dolomite in the present study are too low or the values from Kulp *et al.* (1952) are too high is not known. There is also a discrepancy between the Sr/Ca value of 12 atoms/1000 atoms for Globigerina ooze found by Kulp *et al.* (1952) in contrast to values of 1–3 atoms/1000 atoms found by Chow and Thompson (1953), Turekian and Kulp (1956), and in this study (Figure 6 and Table 23). In a personal communication Turekian indicates that the 1952 samples were not typical Globigerina ooze.

TABLE 29

Strontium in Replaced and Unreplaced Fossil Materials[1]

	Appearance Regarding Degree of Replacement	Sr/Ca Atoms/1000 Atoms
Precambrian		
"*Eozoan canadense*"	?	0.43
Alga? Late Proterozoic, Wyoming, 35% calcium	poor	0.47
Alga? Late Proterozoic, Lake Mislassini, Quebec, 20% calcium	poor	0.36
Cambrian		
Obolus matinalis conglomerate, St. Croix, Minnesota	good	2.60
Dicellomus pellitus, Wisconsin	good	2.32
Dicellomus appalachia Virginia	good	3.70
Pleospongia	poor	0.34
Crypotozoan, New York	poor	0.51
matrix		0.72
Cryptozoan, New York	poor	0.31
matrix		0.41
Ordovician		
Tetracoral, Versaille, Indiana	poor	0.55
Brachiopod, unidentified	fair	1.53
matrix	....	0.48
Devonian		
Stropheodonta	good	1.44
Stropheodonta Genshaw Formation Michigan	fair	0.71
matrix	....	0.53
Mucrospirifer sp., Bell Shale, Michigan	good	1.85
matrix	....	0.85
Athyris sp., Bell Shale, Michigan	good	2.06
Athyris sp., Bell Shale, Michigan	good	1.54
matrix	....	0.50
Athyris sp., Bell Shale, Michigan	good	1.43
matrix, calcite crystal	....	1.05
Athyris spirifironis, New York	good	1.10
Chonetes sp., Bell Shale, Michigan	good	1.56
Cystiphyllium sp., Moscow, Leiscostor, New York	poor	1.19
Heliophyllum sp., Moscow, Leicostor, New York	poor	1.02
Heliophyllum sp.	poor	0.43
Paraspirifer sp., Bell shale, Alpena, Michigan	good	1.14
matrix, shell conglomerate	....	0.70
Bothryolepis sp., Esculminac Bay	good	3.46
matrix	....	1.86
Mississippian		
Ucula nukonis	fair	3.56
Limer waccensis	poor	0.26
Turritella sp., Denison, Texas	fair	4.04
Pennsylvanian		
Echinocrinus megastylios, Topeka, Kansas	poor	0.52
Echinocrinus sp., Topeka, Kansas	poor	0.92
Tetracoral, Fort Leavenworth, Kansas	poor	3.16
Eupaelyerinus sp., Fort Leavenworth, Kansas	fair	1.23
Mixed mollusks, Conemaugh formation, Maryland	good	3.26
Composite sublellita	fair	0.92
Composite ovala	fair	1.57
Pleurophoris sp.	fair	1.02
Pustula symmetricus	fair	1.24
Dictyoclostus americanus	fair	1.02
Dictyoclostus magnicostales	fair	0.85
Productus calardaensis	fair	1.12
matrix	....	1.55
Linoproductus sp.	fair	1.77
Margerifera splendens	good	1.67
Wellerella osagensis	fair	0.53
matrix	....	0.77
Brachiopod, unidentified, Oklahoma	fair	1.55
Lingula umbarata, scrapings	fair	3.32
Snail, unidentified	good	3.60
matrix	....	1.41
Tetracoral	poor	1.22
Nautiloid, contained aragonite, asphalt quarry, Tishomingo Quadrangle, Oklahoma	Excellent	3.67
Nautiloid, Asphalt quarry, Tishomingo Quadrangle,		

Table 29—Continued

Strontium in Replaced and Unreplaced Fossil Materials

	Appearance Regarding Degree of Replacement	Sr/Ca Atoms/1000 Atoms
Oklahoma	Excellent	2.46
Fusulina sp.	fair	2.26
Permian		
Eryops sp. tooth	fair	2.69
Jurassic		
Icthyosaur tooth, Lyme Regis	fair	3.41
matrix	....	1.13
Crocodile bone, Morrison Formation, Wyoming	fair	6.7
Allosaurus sp., Morrison Formation Quarry 9, Como Bluff, Wyoming	fair	7.2
Cretaceous		
Coon Creek Formation, McNary, Tennessee		
Nucula slackiana	good	5.8
Cyprimeria alta	good	3.0
Volulomorpha conradii	good	4.2
Odontofusus medians	good	5.1
Cucullaea tippana	good	3.5
Glycymeris mortoni	good	3.3
Trigonia thoracica	good	3.44
Ostrea falcuta	good	1.80
Crassalellites vadosus	good	7.4
Turritella tippana	good	5.2
Cardium spillmani	good	4.0
Terebratula harlani, Vincentown, New Jersey	fair	2.03
Exogyra costata, Upper Freehold, New Jersey	fair	1.83
Sacculites, Pierre Shale, South Dakota	good	2.96
Belemnite, Monmouth, New Jersey	–?–	2.18
Scaphites sp.	good	3.94
Hyposaurus sp. Greensand, New Jersey	fair	2.05
Exogyra texana, Goodland Formation, Comfort, Texas	good	1.41
Enallaster taxanus, Comige Peak Formation, Clifton, Texas		
outside scrapings	poor	1.00
internal matrix	....	0.80
Eocene		
Nummulites, Florida	poor	0.59
Chlorellopsis colorita, Alga, Faison, Wyoming, 32.8% calcium	good	2.76
Miocene		
Arcillaria obsoleta	good	3.42
Pecten spirula	good	3.02
Conus sp.	good	2.35
Natica millepunctata	good	3.01
Dentalium bornei	good	2.37
Venus plicata	good	3.36
Natica borgalens	good	2.20
Troches palulos	good	2.83
Cancyllaria aculargulala	good	1.33
Pectenuculus stellatus	good	3.66
Coral, Lake Waccamaw, North Carolina	good	11.10
Ostrea sp., Lake Waccamaw, North Carolina	good	1.43
Pecten sp., Lake Waccamaw, North Carolina	good	2.00
Venus sp., Lake Waccamaw, North Carolina	good	2.80
Matrix, Lake Waccamaw, North Carolina	....	1.23
Porites sp., 640 feet, Bikini drilling	good	9.9
Coral unidentified, La Salud, Cuba	poor	1.25
Coral unidentified, Camaguey, Cuba	poor	1.95
Ostrea sp., Cuturre, Cuba	good	1.04
Pleistocene		
Pecten sp., Florida	good	1.90
Turritella sp.	good	3.00
Marginella sp.	good	2.62
Melongema corona	good	2.72
Mittra visciformis	good	1.21
Oliva sayana	good	3.14
Pecten circularis Sowerby Palos Sand, Orange Co., California	good	2.57
Mellita longifissa Michelin, Orange Co., California	superficially good but with cleavage	1.03

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[1] Specimens analyzed for this table were kindly provided by J. Imbrie, J. Wells, C. Prouty, R. L. Cassanova, J. Tracey, M. A. Fritz, C. Waage, C. O. Dunbar, Mrs. A. Knopf. J. Gregory, and the Yale Peabody Museum.

Although Kulp *et al.* (1952) noticed replacement in many specimens and found that the Sr/Ca ratio of a series of unreplaced fossils was higher than a contrasting series of partly replaced specimens, they might have emphasized further the degree of replacement that had taken place in their materials. The entire Table 4 from Kulp *et al.* (1952), seems to contain replaced specimens, except perhaps the phosphatic brachiopod. They discussed strontium with respect to age, horizontal patterns on a strike, and salinity in materials with Sr/Ca ratio less than 1 atom/1000 atoms which were almost certainly replaced. All the echinoderm values, for example, were less than 0.8 atoms/1000 atoms (modern values, 3.8 atoms/1000 atoms) ; many brachiopods had less than 0.6 atoms/1000 atoms in contrast to equivalent modern shells of 1.1–1.8 atoms/1000 atoms. The shells varied in Sr/Ca ratio over a wide range. Since some specimens were as high as modern equivalents, one can not suggest that these data indicate an original low strontium content in the sea. Kulp, Turekian, and Boyd (1952) thought that when matrix and shell were the same, that both were showing original organic values. The reverse is probably the case as described below (strontium in replaced and unreplaced fossils).

New and literature analyses for Sr/Ca ratio of limestones and dolomites are plotted on frequency diagrams in Figures 8 and 9. A logarithmic scale is used in order to condense the horizontal extent of the distribution graph. Where celestite is present, very high Sr/Ca ratios may be expected; where dolomites have formed by replacement and the strontium carried away, very low Sr/Ca ratios may be expected. Thus the bimodal distribution of Sr/Ca ratios in the data from Stout (1941) is not inconsistent with a replacement interpretation.

One may reason that with dolomitization in the presence of sulfates strontium would not be moved from its original position very far before celestite deposition occurred. Thus in evaporite deposits, an overall average of all the various layers might be representative of the original Sr/Ca ratio in the first deposition. Vinogradov and Borovik-Romanova (1945) reported Sr/Ca ratios for many successive layers of an evaporite deposit containing limestone, anhydrite, gypsum and dolomite (Table 28). A weighted overall average was obtained for this deposit by multiplying the strontium and calcium contents of each layer by the thickness of the layer and summing. The overall average Sr/Ca ratio thus computed was 6.2 atoms/1000 atoms.

If deposition had occurred in entirely isolated sea water, a Sr/Ca ratio equal to that of the sea (9.0 atoms/1000 atoms) would be expected. If, however, deposition had occurred with free exchange of water with the open sea, values like those of modern terrigenous sediments might have been expected (1–4 atoms/1000 atoms). Thus the computed Sr/Ca value of 6.2 atoms/1000 atoms is consistent with a deposition in a semi-isolated arm of the sea with some exchange.

Not only dolomites are very low in Sr/Ca ratio; other carbonate rocks like marble known to be much altered are equally low in Sr/Ca ratio. Such patterns suggest the Sr/Ca ratio as a good indicator of replacement in carbonate rocks.

The mean Sr/Ca value of 9 Paleozoic shales extracted with dilute acid was 2.6 atoms/1000 atoms, not much lower than the Sr/Ca ratio found for 4 modern muds (3.9 atoms/1000 atoms). It can be reasoned that shales, being less permeable, are less likely to have been replaced than limestones. Consequently the higher Sr/Ca values in the acid extracts of Paleozoic shales than in extracts of Paleozoic limestones are due to better preservation of original deposition in the shales. Since the carbonate fractions of ancient shales are not much lower in Sr/Ca ratio than modern ones it is difficult to use shales as evidence of a much lower Sr/Ca ratio in the ancient sea as Turekian and Kulp (1956) tried to do.

The Sr/Ca ratio of 3 chalks of possible marine origin was 1.49 atoms/1000 atoms and thus somewhat similar to values of modern fine grained biogenic oozes (Table 21). Presumably these deposits are little replaced. Since at least some of the ancient limestones and shales have Sr/Ca ratios similar to modern deposits, whereas other samples have values many times lower than anything in modern seas, one seems forced to interpret the lower values as a result of replacement. The limestones which retain visibly, recognizable fossils tend to have higher Sr/Ca ratios than similarly consolidated limestones which do not retain any fossiliferous patterns.

STRONTIUM IN REPLACED AND UNREPLACED FOSSILS

The Sr/Ca ratio of fossils have been analyzed with an aim of interpreting the extent of replacement and if possible something about the strontium at time of the deposition. The strontium analyses of fossils and matrices are given in Table 29. Kulp, Turekian, and Boyd (1952) found 1.03 atoms/1000 atoms in fossils in comparison to 0.51 atoms/1000 atoms.

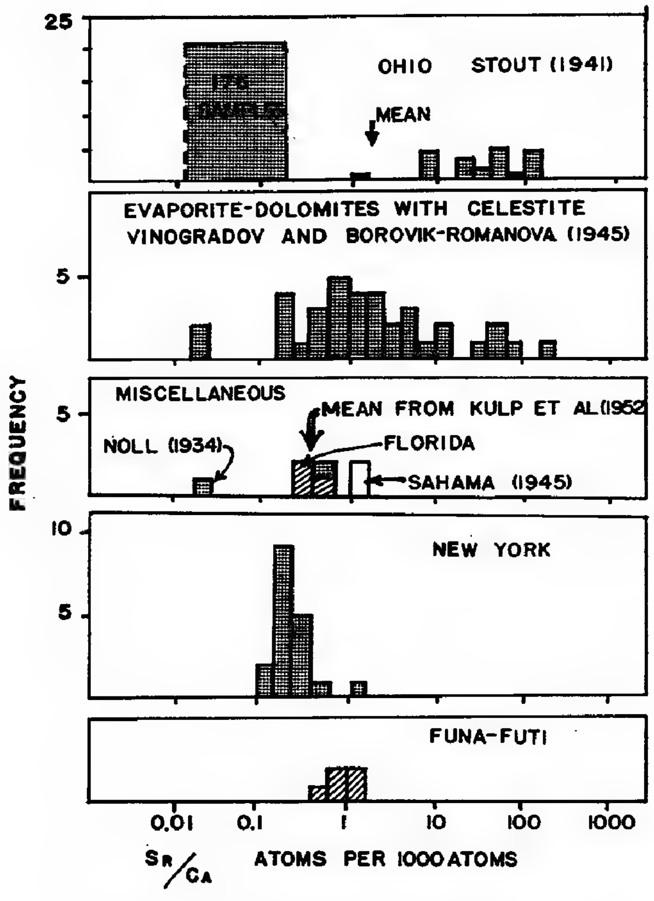

Fig. 8. Sr/Ca ratio in dolomites. Frequency distributions have been plotted for new analyses and literature data.

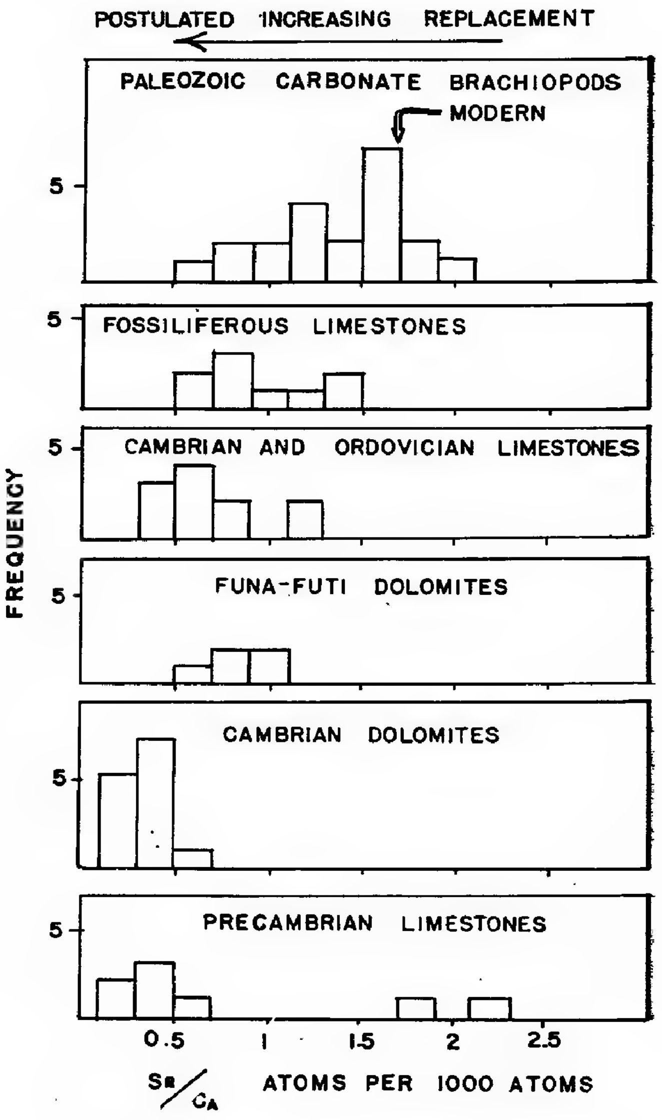

Fig. 9. Sr/Ca ratio in replaced materials.

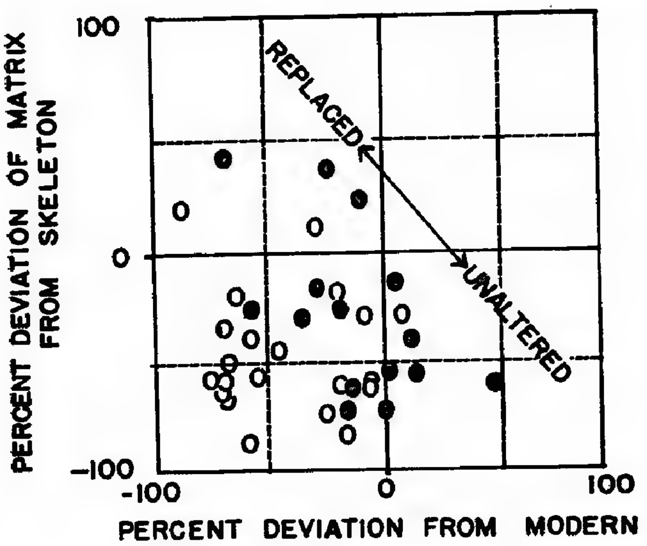

Fig. 10. Sr/Ca ratio in fossils and fossil matrices. Data from this study are black circles and data from Kulp, Turekian, and Boyd (1952) are open circles. These data are plotted on a graph of (a) difference between fossil and matrix versus (b) difference between fossil value and value for equivalent modern skeleton. Most of the fossils have lower Sr/Ca ratios than modern values but higher values than the matrix. A slight trend in the distribution has been interpreted to indicate that replacement results in lowering of Sr/Ca ratio and greater similarity between fossil and matrix.

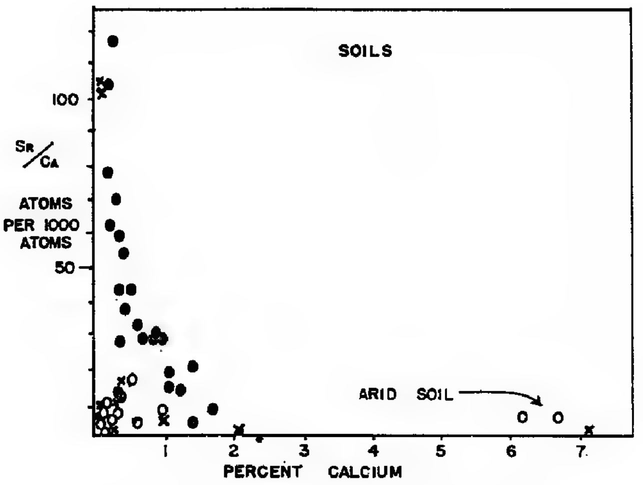

Fig. 11. Sr/Ca ratio of soils as a function of calcium content. Data of this study are open circles; data of Robinson (1914) are black circles; and data of Rogers, Gall, Gaddum, and Barnette (1939) from Florida are crosses.

In the frequency pattern of Sr/Ca ratios of Paleozoic carbonate brachiopods in Figure 9, a very great range is observed in contrast to the much narrowed limits characteristic of recent, calcite, taxonomic groups. Most of the values are equal or less than the modern values of 1.2–1.7 atoms/1000 atoms. Varying degrees of replacement of the brachiopods could produce such a pattern. A similar graph in Kulp, Turekian, and Boyd (1952) should be examined for comparison.

In Figure 10 are presented data on fossils and their matrices. The percent deviation of the Sr/Ca ratio of the skeleton from the matrix is plotted as a function of the percent deviation of the fossil from a modern counterpart. The distribution of points suggests that a fossil and its matrix tend to have similar Sr/Ca ratios when the Sr/Ca values are low. When the Sr/Ca ratios are as high as unreplaced modern shells, the Sr/Ca ratios of the fossils tend to be greater than that of the matrix. This pattern suggests that a difference between the Sr/Ca ratio of fossil and matrix is a useful indication that complete replacement has not occurred.

Echinoderms like corals seem to be easily replaced, much more so than brachiopods and mollusks, probably because of porosity. The familiar cleavage of fossil echinoderms due to interstitial deposition and replacement is easily recognized. It is doubtful if many fossil echinoderms exist which are unreplaced, however well they appear on the outside. For example, three splendid looking Pennsylvanian urchins analyzed had Sr/Ca of 0.89 atoms/1000 atoms in comparison to 3.06 atoms/1000 atoms in 3 modern urchins. No such discrepancy exists between Pennsylvanian and modern mollusca. A very low Sr/Ca ratio (less than 1 atom/1000 atoms) in skeletons is apparently a useful indicator of replacement. Replacement in the Florena shale is discussed relative to analyses by Turekian (See section on strontium in the sediments of open and closed basins). All the fossils discussed by Imbrie (1955) are apparently replaced. The higher strontium in the bottom stratum of the Florena shale may be associated with replacement processes although a correlation with salinity is not ruled out even though specimens are partly replaced.

Additional data on less altered fossils with higher Sr/Ca values given in Table 29 supplement earlier data (Odum, 1951a) suggesting that the Sr/Ca ratio of the ocean was about the same in the Paleozoic as now.

One may summarize some of the methods used to infer whether material is replaced or not as follows: First, material with excellent appearance from unconsolidated sediments should be used. Such material is often flaky resembling an ashed shell and often retains some iridescence. The shell of good material can be separated from the matrix with great ease. Kulp, Turekian, and Boyd (1952) were able to obtain one excellent series of unreplaced fossils from the Miocene in this way. The Sr/Ca values were like the modern ones. Secondly, where possible, aragonite forms should be analyzed after one has demonstrated that the shell is still aragonite. An aragonite condition means that there has been no recrystallization since such recrystallization transforms it into calcite. Since the Sr/Ca ratio is lowered by most replacement, any Sr/Ca value of a fossil may be expected to be too low but rarely too high. A frequency pattern of values is helpful in indicating what value a series of analyses approach as an upper limit. The Brachiopod pattern in Figure 9 is an example. In a fourth approach similar taxonomic forms of modern and past ages are compared. If the Sr/Ca ratio is similar, one may postulate that there has been no replacement and that deposition occurred in a medium not unlike the modern one with respect to alkaline earth content. Especially if the fossil belongs to a taxonomic group with an unusual Sr/Ca ratio, can the similarity in values between the modern and the fossil forms be used to indicate that replacement has not occurred

A fifth means of avoiding the use of replaced materials is to analyze specimens preserved in substances that are impermeable to solutions. Thus material in shales are somewhat more satisfactory than material in limestones. A better technique is to use material imbedded in asphalt as was possible in one case.

A CONTROVERSY CONCERNING THE INTERPRETATION OF THE SR/CA RATIO IN FOSSILS AND THE STRONTIUM CONTENT OF PALEOZOIC SEAS

From the very start of recent interest concerning strontium as a paleoecological tool there has been a doubt regarding the reliability of fossil materials. As reviewed previously the replacement and recrystallization of calcium carbonate materials can change the Sr/Ca ratio markedly in many situations especially towards lower values. Some discussion and concern has been expressed in preceeding papers. (Noll, 1934; Odum, 1950a, 1950b, 1951a, 1951b; Kulp, Turekian and Boyd, 1952; Turekian and Kulp, 1956). Interpretations, heretofore, had mainly been restricted to skeletons which are not porous initially such as brachiopods and molluscs. It was observed as described in the previous sections that specimens from the Paleozoic had Sr/Ca ratios either the same as the modern ones or much lower. Recrystallization seemed to have taken place in most specimens. Only a few still held the higher Sr/Ca ratios representative of original deposition.

When the Paleozoic and calcitic Tetracorals were analyzed (Odum, 1950b; Kulp, Turekian and Boyd, 1952) and found to have an extremely low value relative to Tertiary or modern corals, the low values were interpreted as a result of general replacement of an extremely delicate and originally porous structure. There was, however, always a doubt that tetracorals were drastically different biologically and had originally deposited as a much lower Sr/Ca ratio. By this view the calcite material in Tetracorals was original.

Recently, Bowen (1956a, 1956b) analyzed a new series of Paleozoic corals (0.2–2.8 atoms/1000 atoms) and chose to make the second interpretation. He considered the corals as unreplaced and therefore interpreted the ancient ocean as much lower in Sr/Ca ratio with a gradual increase in strontium since that time relative to calcium. Even if modern calcite corals are used for comparison (2–4 atoms/1000 atoms) there is still a discrepancy.

In their most recent paper Turekian and Kulp (1956) changed their view and postulated Sr/Ca ratios of the ocean increasing with time. Their data on shales do not show this but show only significant differences between their series by epochs in an unsystematic manner. Their discussion based on reported high Sr/Ca values of Foraminifera based on Globigerina ooze analyses are quite in contrast to very low values for foraminifera found in this paper, by Chow and Thompson (1955), Emiliani (1955) and apparently by Turekian and Feely (1956) in later analyses reported in an abstract. The higher values of Sr/Ca ratio obtained in Globigerina ooze with their spectrographic method if accurate may be due to inclusion of high Sr/Ca ratios of insoluble argillaceous fractions as well as the carbonate.

Turekian and Kulp's discussion does not consider the concept of rapidly turning over calcium and strontium cycles in the ocean in approximate steady state (Odum, 1951a). Turekian and Kulp believe igneous rocks to be the source of strontium and calcium for the rivers during geologic time. This belief is probably quite erroneous as most of the alkaline earth elements washing into the sea come from the sedimentary cycle with only 1/20 from the igneous part of the earth cycle. These authors accept the idea of the Paleozoic fauna as more calcite without considering an equally likely possibility that the skeletons are almost all recrystallized. This author is then misquoted regarding the existence of a solid solution of strontium and calcium carbonate.

The controversy is most important because until it is settled to the satisfaction of all the validity of any Sr/Ca interpretations paleoecologically is in doubt. There does not seem to be any possible compromise. One or the other point of view is wrong.

The following are against the interpretation of increasing Sr/Cr ratio in the ocean.

(1) An aragonite Paleozoic nautiloid imbedded in asphalt with original pearly luster showed a Sr/Ca ratio equally high as a modern nautiloid (Odum, 1951a).

(2) In cases analyzed the internal matrix and the scrapings of septa of tetracorals showed the same Sr/Ca ratio as the external matrix whereas most unconsolidated and unreplaced marls show higher Sr/Ca ratio in the skeletons than in the fine grained matrix.

(3) The liklihood of replacement increases with age. Less strontium in older deposits may be thus explained. Replacement of aragonite structures almost always leads to a calcite structure.

(4) The Sr/Ca values for the tetracorals are not only low but are of similar magnitude as limestones and dolomites which are known to be much recrystallized because of the poor condition of other fossils present.

What may solve the question will be an anaylsis of a still porous-definitely unreplaced tetracoral if it exists.

STRONTIUM IN LIMESTONE CORES[1]

Some information on the effect of replacement processes on the Sr/Ca ratio may be obtained from analyses of limestone cores. Data from Key West, Florida, Funa-futi, and Bikini are given in Table 30. The recrystallized foraminifera at 450 ft. in Bikini and casts of corals and algae at 624 ft. at Funa-futi were examined microscopiclly by J. Tracey. The correlation of low Sr/Ca ratio with recrystallization in these samples and in limestones of Key West are consistent. None of the materials of original deposition (2.7 to 11.4 atoms/1000 atoms; Table 29) could have been responsible for such low Sr/Ca values (less than one atom/1000 atoms) without replacement.

To account for the deep and extensive replacements in these limestone beds one might postulate the action of water movement of successive salt water intrusion and extrusion due to fluctuating fresh water table. If during Pleistocene times a drop in sea level of 100 feet had occurred, a fresh water lense up to 4000 feet in depth might be forced downward according to the Ghyben-Herzberg principle.

An example of the low Sr/Ca ratio obtained during a solution and reprecipitation is the value of 0.18 atoms/1000 atoms in calcareous sinter forming under moss in the drainage from a limestone talus (Table 27). Calcium carbonate low in strontium may be most readily found in commercial quantity in marble.

PALEOECOLOGICAL INTERPRETATIONS

The Sr/Ca values in Tables 29–32 can be used in many instances for making paleoecological inferences in terms of what is known about the strontium cycle. The use of strontium analyses to differentiate objects of marine association from objects of fresh water association has occurred to many workers since the large amount of strontium in the sea was discovered. Wilson (1941) used strontium analysis to tell if corrosion of metals was associated with sea water. Similarly strontium analyses of blood have been used to distinguish fresh water drownings from salt water drownings (Severin, 1932). In a similar manner, it is possible to use analyses of Sr/Ca ratios to determine whether

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[1] An unfortunate series of erroneously quoted strontium values on reefs was published in Emery, Tracey, & Ladd (1954). J. Tracey explained the error in a letter as follows: A personal communication from Odum to Tracey giving some first analyses (erroneous) was incorporated into notes in 1949. When in 1950 a standardization error was corrected and the correction sent by Odum, Ladd and Tracey were in the Pacific and the letter was filed and forgotten during the writing. Thus the entire discussion on pages 86 and 87 concerning the reasons why some initial analyses on Bikini are twice too low and do not agree with some others made in the U. S. Geological Survey should be ignored since the error does not exist in any data except that quoted from the personal communication. Values on the Sr/Ca ratio in waters, skeletons, and sediments both in the original thesis and in papers since have agreed approximately with other authors. The data on reefs described in these paragraphs do agree with the other data given in Emery, Tracey and Ladd (1954).

TABLE 30

Strontium in Insular Limestone Cores

	Sr/Ca Atoms/1000 Atoms
Materials at Bikini, samples furnished by H. Ladd, J. Tracey and J. Wells	
4 Hexacorals, Bikini (Table 6)	11.44
Octocoral, *Heliopora sp.*	8.00
Foraminiferan, *Calcarina defrancii*	2.77
Bikini, coral sand	10.89
Bikini, *Halimeda* sand	13.00
Rongerick atoll, sand	3.54
Rongelap atoll, sand	3.65
Foraminiferal ooze on seamount, 720 fathoms, 11.44′, 47″ N. lat.; 165 09′, 56″ E 70% globigerina, 10% *Globorotalia*, 27% others	2.72
Bikini boring:	
116 feet aragonite and calcite	6.17
200 feet	6.99
320 feet unaltered, 40% forams	1.39
450 feet recrystallized forams	0.76
578 feet unaltered forams and mollusks	1.88
640 feet *Porites* aragonite, Miocene	9.90
946 feet aragonite, some calcite	9.63
1140 feet calcite	1.00
Materials at Funa-futi, boring	
100 feet aragonite and calcite	7.83
624 feet calcite, casts of coral and Halimeda	1.54
624 feet dolomite	1.00
646 feet dolomite	0.75
720 feet dolomite	0.61
826 feet dolomite and calcite	1.03
935 feet dolomite	0.70
Materials at Key West, City Well, W-265-Sec 30 T67S, R25E Monroe Co., Fla. Samples furnished by H. Gunter, Florida Geological Survey.	
Surface oolite	10.0
675 feet	1.10
950 feet	1.45
1100 feet	3.10
1225 feet	1.65
1400 feet	0.64
1650 feet	0.60
1750 feet	1.00
1850 feet	0.81
1925 feet	1.02
2325 feet	0.60

TABLE 31

The Use of the Sr/Ca Ratio in Limestone to Determine the Nature of Ancient Environments

Deposit	Sr/Ca Atoms/1000 Atoms	Possible Interpretations From Observed Ratio[a]
Burgess Shale, presumably marine, acid extract	2.30[b]	Saline, volcanic or ground water
Lime Shale, matrix of *Bothryolepis*, Devonian Ostracoderm, presumably freshwater	1.86	Saline or ground water
Conemaugh formation, freshwater limestone, Pennsylvanian of Maryland	0.64	Open freshwater or replaced
Solenhofen limestone, Jurassic; disputed marine, insects, *Limulus*, pycnogonids, birds	0.46 0.5 (Noll, 1934)	Open freshwater or replaced
Kootanie formation, Cretaceous, Elliston Montana, freshwater snails present	0.51	Open freshwater or replaced
Lebanon, limestone, Cretaceous, freshwater, water arachnids	1.20	Open freshwater or replaced
Florissant, Teller Co., Colo., Miocene, with insects	10.60	Saline water, volcanic drainage
Limestone, with arachnid, freshwater, Coconins Co., Arizona	0.20	Open freshwater or replaced

[a] "Saline" may mean marine, arid lake, or mineral water.

[b] In Figure 5 this point could fit with some modern open lake sediments because of the low calcium (2.6%) and the corresponding small carbonate content.

fossil skeletons that are unreplaced are marine or fresh-water (Table 8). There is, however, always the uncertainty that the specimen may have lived in one of the types of localities which have high strontium as discussed in the previous paper (Odum, 1957). If the Sr/Ca ratio is higher than the Sr/Ca of ocean species a non marine locality with a high Sr/Ca ratio can be recognized, but if the Sr/Ca is only slightly high, independent evidence is required for proper interpretation.

Katchenkov (1952) finds higher strontium content in marine sediments than in fresh-water sediments. The method of telling marine from fresh water skeletons is based on the assumption that a similar Sr/Ca ratio existed in past oceans as suggested above. The method can not be used where diagenetic replacement has modified the Sr/Ca ratio. Selection of well preserved material is therefore very important. In Table 32 some analyses of fossils are reported to illustrate the method. Since the closed lakes resemble the oceans in having high strontium content, the Sr/Ca ratio cannot always indicate the difference between inland closed basins of sedimentary drainage and the ocean.

Some of the interpretations given in Table 32 agree with preferred hypotheses about problematical habitats. The freshwater Mason Creek Formation and the freshwater Don beds have low Sr/Ca ratios as do most ordinary fresh waters. The fossils from the Lyme Regis, New Jersey Greensand, Champlain Sea, and James Bay properly show a high Sr/Ca ratio characteristic of saline marine environment.

TABLE 32

The Use of the Sr/Ca Ratio in Fossil Skeletons to Determine the Nature of Ancient Environments

Species, Locality and Remarks	Sr/Ca Atoms/1000 Atoms
Fossils with high Sr/Ca ratio possibly indicating marine, arid lake, ground water source, or volcanic drainage:	
Icthyosaurus sp., Jurassic, Lyme Regus Dorchetshire, England, marine	3.41
Hyposaur, crocodile, New Jersey, Greensand, Cretaceous, marine	2.05
Calcareous algae, *Chlorellops caloritta,* Eocene lake, Green River formation, Wyoming	2.76
Bothryolepis sp., Ostracoderm, Devonian, presumably freshwater?	3.46
Ostrea sp., Livingston formation, Montana, Cretaceous; with dinosaurs	2.22
Saxicava sp., Champlain sea, post glacial, Quebec, presumably marine	1.88
Eryops sp., tooth; Geraldine, Texas, lower Permian	2.69
Unio sp., Oldman River, Alberta; in Livingston range, Cretaceous	1.85
Cretaceous deposit in South Dakota; between layers of marine ammonites; possibly fresh or brackish	
Corbicula nebracensis (clam)	1.57
Fasciolaria scarborough (snail)	3.18
Lunatia subcrassa (snail)	3.14
Fusus dakotensis (snail)	3.10
Mya truncata, James Bay, Post glacial	3.66
Fossils with low Sr/Ca ratios indicating origin in a freshwater of a type which has a low Sr/Ca ratio:	
Toronto interglacial, Don beds: presumably freshwater	
Quadrula pustulata	1.08
Fusconia undata	1.16
Amblema plicata	1.38
Limpsilis siliquoida	0.90
Snail, Mazon Creek, Illinois, Pennsylvanian, with insects and plants probably freshwater	1.15

Several other more controversial cases analyzed (Table 32) have relatively high Sr/Ca ratios equal to modern marine species. In these cases a marine or brackish water environment might be implied if there were not some independent evidences that the localities were not marine. The Sr/Ca ratio can not be used as a completely definitive answer in these cases because there are a few rare types of water of inland derivation which have as high Sr/Ca ratios as marine waters. The following involve Sr/Ca ratios suggestive of marine conditions: *Ostrea* from the Livingston Formation associated with dinosaurs. *Bothyrolepis* from the Devonian Escuminac Bay formation. Mollusks from the Cretaceous of South Dakota. The high Sr/Ca value in a calcareous alga from the Eocene Green River formation is consistent with derivation from a closed, saline lake environment (Bradley, 1926, 1929, 1948).

The Jurassic Morrison Formation (Table 29) has fossils with twice the Sr/Ca ratio of equivalent modern species. These deposits are impregnated with uranium. Uranium and strontium are both concentrated in pegmatites. Drainage from such substrates may have been involved either during or after deposition.

Most of the best Miocene, Cretaceous, Pennsylvanian, and Devonian fossils reported in Tables 29 and 32 seem to be similar in Sr/Ca ratio to modern skeletons with the exception of the Cretaceous Tennessee Coon Creek Formation where the values are higher for ancient mollusks than for modern ones. The particular Cretaceous sea containing these forms may have been a closed basin.

In Table 31 use is made of the Sr/Ca ratio in sediments for determining past environmental characteristics just as for skeletons. Although each analysis is open to several interpretations such as the ones given in Table 31, the Sr/Ca ratio does help to eliminate some possibilities. The ratio is not a complete answer but in many cases with other sources of evidence can be helpful. At other times the Sr/Ca ratio may be used to indicate prior chemical replacement.

SR/CA RATIO IN WEATHERING AND SOILS

Whereas there seems to be abundant evidence of a lowered Sr/Ca ratio in the replacement and recrystallization of limestones, the weathering of other rocks in the process of formation of soils leads to a high Sr/Ca ratio in the residual material.

Bertrand and Silberstein (1928) noted strontium qualitatively in soils. Robinson (1914) on a series of 26 soils from humid area, found very high Sr/Ca ratios. The absolute concentrations in soils ranged from 0.013—.266% of the dry soil which is in the same range as the absolute concentrations reported by Vinogradov (1945). Allison and Gaddum (1940) compared soils in the U. S. with Florida soils with 0.001–0.1% strontium (Rogers, Gall, Gaddum, and Barnette 1939). Butler (1954) found 0.005–0.013% strontium in English soils. Noll (1931a, 1934) and Gordon and Murata (1952) had speculated on relative absorption of different ions in soils and sediments

TABLE 33

Strontium in Exchange Experiments with 1.0M $CaCl_2$ and Sr/Ca 5.0/1000

Material	Sr/Ca Ratio of Bound Fraction Atoms/1000 Atoms	Calcium Exchange Capacity Millequivalents/100 Grams
Fibrous peat, Singletary Lake, N.C.	4.6	91.0
Bentonite	5.0	42.0
Suffield clay loam	5.3	1.6
Hadley Harbor, marine mud	4.2[a]	7.4
Silt mud containing ferric hydroxide, University Lake, N.C.	4.6	3.5
Kaolin	5.2	65.0
Egg Albumin	1.68	24.5

[a] Corrected for initial calcium and strontium carbonate content.

and concluded that strontium was held differentially. These authors correlate the behavior of cations in these exchange processes to the scale of ionic potential. Following Cartledge (1929) and Goldschmidt (1937), the ionic potential is the ratio of the valence to the ionic radius. The ionic potential of strontium is 1.57, that of calcium is 1.87. Turekian and Kulp (1956) interpreted some high Sr/Ca ratios in shales as due to selective retention of strontium in ion exchange. It was thought that there differential adsorption initially was followed by stronger binding in later consolidation.

In general the loss of alkaline earths from rocks in the process of weathering has been well known (Payne, 1946) but the relative loss of strontium and calcium was not clear although the analyses suggested some mechanism retaining strontium more than calcium in weathering. However, evidence was quoted indicating that strontium is more easily taken up than calcium and also more easily displaced with a net tendency to be lost during exchange. Barbier, Chabannes and Miallet (1946) found calcium absorbed on clay more rapidly than strontium. Wiklander (1946) found Sr more readily exchanged than calcium. Rios and Ruiz found strontium bound more than calcium. Carritt and Goodgal (1954) found that strontium uptake on suspended clay materials followed a Freundlich isotherm pattern. Nishita *et al.* (1956b), found 90% of the tracer strontium taken up on clays was readily leached out.

In this study a few base exchange experiments were carried out on some diversified materials to see if there was a differential binding of strontium relative to calcium in comparison to the Sr/Ca ratio in percolating waters. Five materials typical of soils and sediments were equilibrated with 1.0M $CaCl_2$ solutions which had a Sr/Ca ratio of 5.0 atoms/1000 atoms. Excess solution was removed with large volumes of distilled water and the remaining material extracted with hydrochloric acid, reprecipitated, and analyzed in the usual way. The results of these experiments reported in Table 33 suggest that any differential binding by inorganic or humic material is small or not significant. Thus no evidence was found that the higher Sr/Ca ratios reported for soils are to be attributed to base exchange differential binding by clay minerals.

In order to identify the fraction containing a high Sr/Ca ratio, a study was made of soil components as was similarly made for sediments. Acid extracts and sodium carbonate fusions of residues were analyzed separately. The results of these analyses are reported in Table 34. Just as in the sediments, the acid insoluble fraction is high in Sr/Ca ratio whereas the soluble fraction has a low value of Sr/Ca. It therefore seems that the high Sr/Ca ratio of humid soils is due to the high Sr/Ca ratios in residual insoluble minerals like silicates. Because humid soils are usually exposed to continual leaching, base exchange components, carbonate components, and other soluble components are at a minimum as indicated by the low calcium content of acid extracts (Table 34). The residual minerals include resistant minerals such as alkali feldspars which have extremely high Sr/Ca ratios (1–1000 atoms/1000 atoms). Gordon and Murata (1952) found 0.027% strontium and 1% calcium in nepheline syenite before weathering. After weathering the residual bauxite had 0.019% strontium and 0.12% calcium. The Sr/Ca ratio increased in weathering presumably due to retention of resistant minerals which have a high Sr/Ca ratio. The calcium silicates are more soluble and are expected to be less common in these resistates (Jackson *et al.*, 1948).

The difference between humid soils and sediments therefore is in the percent calcium in relatively soluble form. A soil has lost much of its acid soluble fraction; most sediments have not. There is an interesting similarity between terrestrial soils of humid

TABLE 34

Strontium in Soil Components

	Acid Extract		Residue Na_2CO_3 Fusion		Total	
	Calcium Per Cent	Sr/Ca Atoms/1000 Atoms	Calcium Per Cent	Sr/Ca Atoms/1000 Atoms	Calcium Per Cent	Sr/Ca Atoms/1000 Atoms
Connecticut soils from Triassic sediments of basic origin[a]						
Enfield fine sandy loam	0.06	2.11	0.94	8.2	1.00	7.8
Windsor fine sandy loam	0.04	0.56	0.17	7.5	0.21	6.1
Wethersfield loam	0.11	1.29	0.02	31.9	0.13	6.0
Cheshire fine sandy loam	0.007	1.14	0.45	4.0	0.46	4.0
Suffield clay loam	0.016	3.0	0.37	16.3	0.39	15.6
Profile Hermon stony sandy loam, Yale Forest, Keene, New Hampshire[b]						
A Horizon 0–3 inches	0.007	4.36	0.20	7.1	0.21	6.9
B Horizon 3–12 inches	0.021	2.20	0.03	4.8	0.05	3.7
C Horizon 12–18 inches	0.013	2.31	0.26	5.2	0.27	5.2
Arid Soil						
Houston black clay, Taylor, Williamson Co., Texas[b]						
0–12 inches	4.65	1.53	1.54	18.4	6.19	5.7
24–36 inches	4.91	1.82	1.81	12.2	6.72	4.6
70 inches	6.77	2.52	1.81	9.9	8.58	4.1
Mean of Arid Soils	5.44	1.95	1.72	13.5	7.16	4.8
Mean of Humid Soils	0.034	2.12	0.31	10.6	0.34	6.9
Mean of 26 Humid Soils from many areas, Robinson (1914)	......	......	......	......	0.49	52.5
Florida Soils, Rogers, Gall, Gaddum and Barnette (1939)	......	......	......	......	0.06–7.2	0.6–300

[a] Samples from the Connecticut Agricultural Experiment Station.
[b] Samples from H. J. Lutz.

regions and oceanic red clay, for both are low in carbonates. The Sr/Ca values of the soils analyzed in this study are considerably lower than the Sr/Ca ratios of soils reported by Robinson. Part of this difference may be in the source rock. The soils in this study were from central Connecticut where Sr/Ca ratios in the Triassic sediments and in the basic intrusions from which a good part of these soils was derived are low. Robinson's soils on the other hand include soils derived from many rocks of higher Sr/Ca ratio.

Rogers, Gall, Gaddum and Barnette (1939) found strontium in considerable variation in the soils of Florida. The Sr/Ca ratio varied less than the absolute concentrations of alkaline earths. The range of Sr/Ca from 0.62 in a poorly drained lime soil to 300 atoms/1000 atoms in cultivated soils in nevertheless large. These data confirm Robinson (1914) and indicate a similarity of strontium content in Florida soils and the soils of the eastern U. S. seacoast analyzed by Robinson. Allison and Gaddum (1940) and Carrigan and Rogers (1940) analyzed soils of prairie, chernozem, lateritic, podzol, and peat types from the U. S. and compared these to Florida soils. In general the Florida soils had lower absolute contents. The Sr/Ca ratios however, were in the same ranges as other published data. As shown in Figure 11 the Florida data seem to be accounted for by the theory of soluble and insoluble components discussed in relation to Table 34.

An analysis of the Sr/Ca ratio of three levels in an arid soil (Houston black clay) is included in Table 34. Whereas the acid-soluble calcium containing component of humid soils is very small, arid soils contain much calcium carbonate. The Sr/Ca ratio in the insoluble fraction of the arid soil is similar to the Sr/Ca of the insoluble fractions of humid soils (Table 34). The Sr/Ca ratio of the carbonate part of the arid soil is higher.

The arid soils may be compared to arid lake sediments since both materials contain carbonate components with relatively high Sr/Ca ratios and since both materials form from evaporation. One may thus consider the hardpan layer as the sediments of a tiny lake, the soil water constituting the lake. If the calcium carbonate were precipitating from a solution which was passing through and out of the system the Sr/Ca ratio would be expected to be lower as in the sedimentary deposition of calcite in open waters or in ground water systems in which the water passes through. In one humid soil with a high calcium content from Florida (Figure 11) there is a low Sr/Ca ratio characteristic of limestones. The comparison of a soil solution to a lake may be a useful concept for other soil problems. The correlation of strontium and salt observed in waters may also exist in soils. Miyake (1914) discussed rice plants with high strontium being grown on alkali soils.

Figure 11 summarizes the variation of Sr/Ca in soils. The inverse relationship of Sr/Ca and calcium is noted again as in sediments and rocks. Again this pattern is to be interpreted as an outcome of the differences in geochemical behavior of strontium and calcium. The factors that concentrate one element decrease the ratio of other elements to it. The pattern that results from adding calcium-containing minerals and non-calcium minerals is an inverse curve.

HYPERBOLIC PATTERNS OF SR/CA RATIO WITH CALCIUM

Following a suggestion originally made by G. E. Hutchinson a plot of Sr/Ca ratio verses calcium produced a hyperbolic-shaped curve in many earth phases such as in igneous rocks and the waters from a single geochemical region (Odum, 1950b), lake sediments (Figure 5), marine sediments (Figures 6 and 7), and soils (Figure 11). Menzel (1954) demonstrated a similar distribution when he plotted Sr/Ca ratios against the reciprocal of calcium to obtain a straight line in ions taken up in plants.

Turekian and Kulp (1956) plotted the logarithm of the Sr/Ca ratio of shales and schists against the logarithm of the calcium present obtaining a linear inverse trend which they interpreted as fortuitous. However, the relationship may be theoretically accounted for as follows. The hyperbolic relationship of the ratio of two elements to the one indicated in the denominator is predictable with an equation in any case where there is an admixture of two components in various proportions (Odum, 1950b). In the cases aforementioned there is an admixture of the soluble carbonate component characterized by low Sr/Ca ratio and a less soluble component characterized by a high Sr/Ca ratio. A double logarithmic plot of a hyperbolic relationship is a straight line. Double logarithmic plots readily hide relationships involving products and dividends.

6. Summary

1. 900 analyses of the Sr/Ca ratio of minerals, tissues, skeletons, fossil sediments, rocks, and soils were compared with data in the literature in order to characterize the present and past processes of deposition of strontium.

2. In order to permit comparisons between types of materials and various workers and materials in the literature, all analyses were made with flame spectrophotometric emission methods on strontium and calcium carbonates dissolved in 20% hydrochloric

acid. All samples which were not already in calcium carbonate form, or which contained appreciable foreign elements such as soils, limestones, dolomites, tissues, phosphates, and sediments were ashed, extracted with acid, precipitated with excess oxalate, and ashed back to carbonate thus separating the calcium and strontium from other elements which might have interfered with flame emission.

3. The reproducibility of the reprecipitation procedure as well as the variation in methods and in skeletal materials were measured with an analysis of variance of 48 duplicate analyses of 6 *Venus* clam shells. The average error was 5%.

4. The principal factor controlling the inorganic deposition of strontium minerals, the Sr/Ca ratio in other minerals and the Sr/Ca ratio in carbonate and phosphate skeletons is the Sr/Ca ratio of the depositional environment. The action of the ionic radius principle which predicts co-deposition of strontium and potassium in minerals due to similarity of ionic radius results from the association of the two elements in fluids due to the co-exclusion from previous depositional processes in the geochemical cycle.

5. More strontium was found in aragonite than calcite forms of calcium carbonate minerals and skeletons as found by other workers, although many factors were found to be more important. The correlation is good only on an overall average basis. No evidence was found to indicate that the amounts of strontium usually present in nature determine whether deposition of aragonite or calcite occurs.

6. The Sr/Ca ratio is characteristic of a species or a taxonomic group only when grown with a characteristic Sr/Ca ratio in the external medium or food supply. The Sr/Ca ratio of marine skeletons is much greater than the Sr/Ca ratio of skeletons from those fresh waters which are low in Sr/Ca ratio. The Sr/Ca ratio in terrestrial animals is a function of the Sr/Ca ratio of the food. Analyses of Sr/Ca ratios in marine skeletons further establish the characteristic exclusion factors between medium and skeleton ratios of many taxonomic groups with essential agreement with most previous work.

7. The rate of turnover of alkaline earth elements within the tissues around the depositional site of the skeleton is suggested as a principle factor controlling the Sr/Ca ratio of a species.

8. In animal tissues the Sr/Ca ratio is the same or less than that of the medium and food. The Sr/Ca ratio decreases with decreasing fluid content. There is greater exclusion of strontium relative to calcium in marine than freshwater animals.

9. Comparisons of Sr/Ca ratios in plants and environmental bog waters confirm previous studies indicating that most plant tissues apparently have Sr/Ca ratios similar to those in the media around the roots. The four fold increase of Sr/Ca ratio within brown algae is verified.

10. The Sr/Ca ratio of silicious sponges depends on calcareous inclusions; the Sr/Ca ratio of pelagic forminifera is lower than in most skeletons. Echinoderms are very uniform in Sr/Ca ratio; Gastropods are very varied in Sr/Ca ratio; Lithothamnion and *Polynices* do not vary greatly in Sr/Ca ratio with temperature of environment. Sr/Ca values of phosphate skeletons are similar in order of magnitude to those of carbonate skeletons. Sr/Ca ratios of egg shells reflect the Sr/Ca ratio of the diet.

11. The Sr/Ca ratio of the calcareous, acid-extractable part of fresh water and marine sediments is less than the Sr/Ca ratio of the water above. Higher Sr/Ca ratios are found in the sediments of closed basins than in the sediments of overflowing basins thus indicating dryness of climate.

12. The total Sr/Ca ratio of soils and sediments also depends on the Sr/Ca ratio of the resistant and insoluble fractions which contain a higher Sr/Ca ratio. These values were observed in sodium carbonate fusions of acid-extracted residues. When carbonate fractions are small the overall Sr/Ca ratio of sediments tends to be greater because of the acid insoluble fraction.

13. Sedimentary phosphate deposits of the continental type are characterized by low Sr/Ca ratios because of secondary, replacement processes; oceanic phosphate deposits derived from guano are low in Sr/Ca ratio because of the fish diets of guano birds. High Sr/Ca ratio are found in phosphate deposits where mixed with coral rock because of the high Sr/Ca ratios of the coral.

14. Direct and rapid deposition of calcium carbonate from waters tends to produce as high Sr/Ca ratios as the medium. Oolites, beach rock, Drewite, reef corals, and green aragonite algae all have high Sr/Ca ratios that may be related to rapid deposition of carbonates associated with photosynthesis processes.

15. Analyses of limestones, reef cores, limestone precursors and fossils indicate that replacement and recrystallization lowers the Sr/Ca ratio. The low Sr/Ca values of dolomites may indicate a recrystallization origin.

16. Some Paleozoic materials which have been suggested by several authors as indicating a lower Sr/Ca ratio in the Paleozoic ocean are reinterpreted as lower because of various degrees of replacement and recrystallization.

17. The Sr/Ca ratio as a paleoecological tool may be used under carefully specified conditions in conjunction with other information to indicate (1) replacement, (2) the origin of a deposit from marine or non-marine environments, (3) the climate, (4) food habits.

18. The high Sr/Ca ratio of soils is confirmed and found to be due to the high Sr/Ca ratio of insoluble and resistant minerals like feldspars left in leaching. No evidence is found for concentration of the Sr/Ca ratio in soil by selective retention of strontium from percolating waters.

19. The hyperbolic pattern of the Sr/Ca ratio when plotted against calcium in many types of material is thought to be due to the mixing of the soluble component (with low Sr/Ca ratio) in various proportions with an insoluble fraction (high in Sr/Ca ratio).

20. Mention is made of the unsatisfactory state of present knowledge about strontium with respect to (a) the biochemistry of the Acantharia, (b) the original strontium content of tetracorals, (c) the functional significance of strontium in mold, (d) the wide range of Sr/Ca ratios in coal and oil.

LITERATURE CITED

Ahrens, L. H., 1944. Trace elements in clays. S. Afr. J. Sci., 41: 152–160.

————, 1948. The geochemistry of radiogenic strontium. Miner. Mag., 28: 277–295.

Albrecht, Wm. A., and R. A. Schroeder, 1942. Plant nutrition and the hydrogen ion. Soil Sci., 53: 313–327.

Allison, R. V., and L. W. Gaddum, 1940. The trace element content of some important soils, a comparison. Proc. Soil Sci. Soc. Fla., 2: 68–103.

Andrée, K., 1914. Über den Cölestin in Mokattamkalk von Ägypten. Neues Jb. Min. Geol., 37: 343–390.

Armstrong, E. F., and L. M. Miall, 1945. Raw Materials from the Sea. Leicester, England, Constructive Publishers, 164 pp.

Banks, E. M., and H. T. Odum, 1957. Strontium Deposition in Egg Shells. Tex. J. Sci., 9: 215–218.

Barbier, G., J. Chabannes, and P. Miallet, 1946. Adsorption of phosphate ions at the surface of clay colloids by medium of the alkaline earth metals. Ann. Agron., Paris, 16: 7–33.

Bastin, E. S., and H. Trimble, 1897. A contribution to the knowledge of some North American Coniferae. Amer. J. Pharm., 69: 90–97; 354–359.

Bertrand, G., and L. Silberstein, 1928. Sur la presence ordinaire du baryum et probablement du strontium, dans la terre arable. C. R. Acad. Sci., Paris, 186: 335–338.

Bloom, M. C., and M. J. Buerger, 1937. On the genesis of polymorphous forms-Sb_2O_3. Z. Kristallogr. 96: 365–375.

Borroughs, H. J., S. J. Townsley, and R. W. Hiatt, 1956. The metabolism of radionuclides by marine organisms. I. The uptake, accumulation, and loss of strontium 89 by fishes. Biol. Bull., Wood's Hole, 111: 336–351.

Bowen, H. J. M., 1956a. The biogeochemistry of strontium. Advanc. Sci., Lond., 12: 585–588.

————, 1956b. Strontium and barium in sea water and marine organisms. J. Mar. Biol. Ass. U.K., 35: 451–460.

Bowen, H. J. M., and J. A. Dymond, 1955. Strontium and barium in plants and soils. Proc. Roy. Soc. Ser. B, 114: 355–.... .

————, 1956. The uptake of calcium and strontium by plants from soils and nutrient solutions. J. Expt. Bot., 7: 264–272.

Bradley, W. H., 1926. Shore phases of the Green River formation in northern Sweetwater County, Wyoming. Prof. Pap. U. S. Geol. Surv., 140-D: 121–131.

Bradley, W. H., 1929. Algae reefs and oolites of the Green River formation. Prof. Pap. U. S. Geol. Surv., 154-G: 203–223.

————, 1948. Limnology and the Eocene lakes of the Rocky Mountain region. Bull. Geol. Soc. Amer., 59: 635–648.

Brown, L. S., 1931. Cap-Rock Petrography. Bull. Amer. Ass. Petrol. Geol., 15: 509–529.

Butler, J. R., 1954. Trace element distribution in some Lancashire soils. J. Soil Sci., 5: 156–172.

Bütschli, O., 1906. Über die chemische Natur der Skelettsubstanz der Acantharia. Zool. Anz. 30: 784–789.

————, 1907. Chemische Natur der Skelettsubstanz des *Podactinelius* und der Acantharia uberhaupt. Dtsch. Südpol. Exped. 9; Zoologie, 1: 237–257.

Carrigan, R. A., and L. H. Rogers, 1940. The trace element content of certain Florida soils and related materials. Proc. Soil Sci. Soc., Fla., 2: 92–103.

Carritt, D. E., and Sol Goodgal, 1954. Sorption reactions and some ecological implications. Deep Sea Res., 1: 224–243.

Cartledge, G. H., 1928. Studies on the periodic system. I. The ionic potential as a periodic function. J. Amer. Chem. Soc., 50: 2855–2863.

Cathrein, A., 1888. Ueber calicostrontianit (Emmonit) von Brixlegg. Z. Kristallogr., 14: 366–374.

Chave, K., 1954 Aspects of the biogeochemistry of magnesium. I. Calcareous marine organisms, Jour. Geol., 62: 266–283.

Chilingar, George V., 1956. Relationship between Ca/Mg Ratio and Geologie Age. Bull. Amer. Ass. Petrol. Geol., 40: 2256–2266.

Chipman, Walter A., 1956. Passage of fission products through the skin of tuna. Spec. Sci. Rep. U. S. Fish Willdl. Serv., 167: 1–6.

Clarke, F. W., 1915. Analyses of rocks and minerals, 1880–1914. U. S. Geol. Surv. Bull. 591: 1–376.

————, 1924. The data of geochemistry. 5th ed. Bull. U. S. Geol. Surv., 770: 1–841.

Clarke, F. W., and W. C. Wheeler, 1922. The inorganic constituents of marine invertebrates. Prof. Pap. U. S. Geol. Surv., 124: 1–62.

Collander, R., 1930. Permeabilitätsstudien an *Chara ceratophylla*. Acta Bot. Fenn., 6: 1–20.

————, 1936. Der Zellsaft der Characeen. Protoplasma, 25: 201–210.

————, 1937. Über die Kationenelektion der höheren Pflanzen. Ber. Dtsch. Bot. ges., 55: 74–81.

————, 1939. Permeabilitätsstudien an Characeen. Protoplasma, 33: 215–257.

————, 1941a. Distribution of different cations between root and shoot. Acta Bot. Fenn. 29: 1–12.

————, 1941b. Selective absorption of cations by higher plants. Plant Physiol., 16: 691–720.

————, 1941c. Die Elektrolyt-Permeabilität und Salz-Akkumulation pflanzlicher Zellen. Tabulae Biol. Periodicae Berlinz, 19: 313–333.

Collip, J. B., 1920. The alkali reserve of marine fish and invertebrates. J. Biol. Chem., 44: 329–344.

Collot, L., 1905. Diffusion du baryum et du strontium dans les terrains sedimentaires; epigenies; druses d'apparence organique. C. R. Acad. Sci., Paris, 141: 832–834.

Cormier, R. F., L. F. Herzog, W. H. Pinson, and P. M. Hurley, 1956. Rubidium-strontium age determinations on the mineral glauconite (Abstract). Bull. Geol. Soc. Amer., 67: 1681.

Dietz, R. S., K. O. Emery, and F. P. Shepard, 1942. Phosphorite deposits on the sea floor off southern California. Bull. Geol. Soc. Amer., 53: 815–48.

Dieulafait, L., 1877. La strontiane, sa diffusion dans la nature minerale et dans la nature vivante, a l'epoque actuelle et dans la serie des temps geologiques. Consequences relatives aux eaux minerales saliferes. C. R. Acad. Sci., Paris, 84: 1303.

Dinger, K., 1929. Über die Herkunft des Strontiums in den Schichten des unteren Muschelkalkes und des Röt in der Umgebung von Jena. Chem. D. Erde, 4: 167–177.

Doelter y Cisterich, C. A. 1912–1925. Handbuch der Mineralchemie. Dresden and Leipzig, Steinkopff,

Dugal, L. P. 1939. The use of calcareous shell to buffer the product of anaerobic glycolysis in *Venus mercenaria.* J. Cell. Comp. Physiol., 13, 235–51.

Durell, C. 1953. Geological investigations of strontium deposits in southern California. Spec. Rep. Calif. Div. of Mines, 32: 1–48.

Eardley, A. J. 1938. Sediments of Great Salt Lake, Utah. Bull. Amer. Assn. Petrol. Geol. 22: 1305–1411.

Emery, K. O. and D. C. Cox. 1956. Beachrock in the Hawaiian Islands. Pacif. Sci. 10: 382–402.

Emery, K. O. and R. S. Dietz. 1950. Submarine phosphorite deposits off California and Mexico. Calif. J. Min., 46: 7–15.

Emery, K. O., J. L. Tracey, Jr. and H. S. Ladd. 1954. Geology of Bikini and Nearby Atolls, Part 1, Geology. Prof. Pap. U. S. Geol. Surv., 260–A; 1–261.

Emiliani, C. 1955. Mineralogical and chemical composition of the tests of certain pelagic foraminifera. Micropaleontology, 1: 377–380.

Engelbach, T. 1862. Zur Nachweisung des Baryts und Strontians in Kalksteinen. Ann. Chem. Pharma., 123: 255–261.

Eskola, P. 1922. The silicates of strontium and barium. Amer. J. Sci., ser. 5, 4: 331–375.

Eyerman, John. 1904. Contributions to mineralogy. Amer. Geol., 34: 43–48.

Faivre, Rene. 1944. Studies, by X-ray diffraction and dilatometric analysis, of mixed carbonates of calcium and strontium and their transformations. C. R. Acad. Sci., Paris., 219: 73–74.

Fay, Marion, M. A. Andersch, and V. G. Behrmann. 1942. The biochemistry of strontium. J. Biol. Chem., 144: 383–392.

Fersman, A. E. 1926. Minerals of the Kola Peninsula. Amer. Min. 11: 289–299.
1929. Geochemische Migation der Elemente 1. Agpaitische Pegmatite der Halbinsel Kola. Abh. Prakt. Geol. Bengw., 18: 21–73.

Finkel, M. P. 1947. The transmission of radiostrontium and plutonium from mother to offspring in laboratory animals. Physiol. Zoöl., 20: 405–421.

Forchhammer, G. 1844. On the influence of fucoidal plants upon the formations of the earth, on metamorphism in general, and particularly the metamorphosis of the Scandinavian alum slate. Rep. Brit. Assn. (1844) : 155.
1865. On the composition of sea water in the different parts of the ocean. Phil. Trans., 155: 203–262.

Fox, H. M., and H. Ramage. 1931 A spectrographic analysis of animal tissues. Proc. Roy. Soc. Ser. B., 108: 157–173.

Fretter, V. 1953. Experiments with radioactive strontium 90 on certain mollusks and polychaetes. J. Mar. Biol. Assn. U.K., 32: 367–384.

Gallo, G. 1935 Equilibrium of strontium sulfate and water at various temperatures. Ann. Chim. Appl., Roma, 25: 628–631.

Genth, F. A. 1852–1853. On strontiano-calcite, a new mineral. Proc. Acad. Nat. Sci. Phila., 6: 114.

Goldschmidt, V. M. 1937. The principles of distribution of chemical elements in minerals and rocks. J. Chem. Soc. 140, pt. 1: 655–673.

———— 1954. Geochemistry. Oxford, Clarendon Press, 730 pp.

Gordon, M. and K. J. Murata. 1952. Minor elements in Arkansas bauxite. Econ. Geol., 47: 169–179.

Graf, D. L. and J. E. Lamar. 1955. Properties of calcium and magnesium carbonates and their bearing on some uses of carbonate rocks. Econ. Geol., 50: 639–713.

Grahmann, W. 1920. Über Barytöcolestin und das Verhältnis von Anhydrit zu Cölestin und Baryt. Neues Jb. Min. Geol. Paläont., (1920) : 1–23.

Grawe, O. R., and M. P. Nackowski. 1949. Strontianite and Witherite associated with southern Illinois fluorite. Science, 110: 331.

Gray, A. N. 1943. Phosphates and Superphosphate. New York, Interscience Publishers, 416 pp.

Greenberg, D. M. 1945. Studies in mineral metabolism with the aid of artificial radioactive isotopes. VIII. Tracer experiments with radioactive calcium and strontium on the mechanism of vitamin D action in rachitic rats. J. Biol. Chem., 157: 99–104.

Grosch, D. S., and L. E. LeChance. 1956. Fate of radiostrontium fed to Habrobracon females. Science, 123 (3187) : 141–142.

Guichard, M., and J. Wyart. 1943. Structure crystallographique des melanges de carbonates de calcium et de strontium precipites. Leur decomposition fractionee par la chaleur. C. R. Acad. Sci., Paris, 216: 844–846.

Hadding, A. 1939. Barites and celestite in the sedimentary rocks of Sweden. K. fysiogr. Sällsk. Lund Förch., 8: 83–109.

Hardin, G. C., and W. R. Thurston. 1945. Celestite from Livingstone County, Kentucky. Amer. Min., 30: 639–640.

Harness, C. L. 1949. Strontium minerals. In Industrial Minerals and Rocks, Amer. Inst. of Mining and Metallurgical Engineers, York, Pennsylvania, Maple Press, pp. 980–988.

Haselhoff, E. 1893. Versuche uber den Ersatz des Kalkes durch Strontium bei der Pflanzenernährung. Landw. Jb., 22: 851–857.

Hevesy, Von G. von and K. Würstlin. 1934. Uber die Häufigkeit des Strontiums. Z. Anorg. Chem., 216: 312–313.

Hill, J. M. 1916. Strontium in Mineral Resources of the United States, pt. 2, pp. 185–195.

Hillebrand W. F., and G. E. F. Lundell. 1929. Applied Inorganic Analysis. New York, J. Wiley and Sons. 929 pp.

Hintze, C. 1886. Ueber Cölestin von Lüneburg und das Studium von Vicinalflächen. Z. Krystallogr., 11: 220–235.

Hintze, C. and Linck, G. 1930. Handbuch der Mineralogie. Berlin and Leipzig. Walter de Gruyter and Co., Vol. 1, div. 3, No. 1: 2677–3656.

Hodel, Ernst. 1925. Zur Biochemie der Erdalkalien. Helv. Chim. Acta, 8: 514–518.

Hodge, H. C., E. Gavett, and I. Thomas. 1946. The adsorption of strontium at forty degrees by enamel, dentin, bone and hydroxyapatite as shown by the radioactive isotope. J. Biol. Chem., 163: 1–6.

Hodges, R. M., N. S. Macdonald, C. McArthur, P. Spain, F. Ezmirlian, R. Nusbaum, and R. Stearns. 1949. The strontium content of human bones. Univ. California School of Med. Atomic Energy Project, No. At-04-1-Gen-12: 1–16.

Hodges, R. M., N. S. Macdonald, R. Nusbaum, R. Stearns, F. Ezmirlian, P. Spain, C. McArthur. 1950. The strontium content of human bones. J. Biol. Chem., 185: 519–524.

Holmes, A. and Harwood, H. F. 1932. Petrology of the volcanic fields east and southeast of Ruwenzori, Uganda. Quart. J. Geol. Soc. Lond., 88: 370–442.

Hopkins, R. H. 1942. The dolomitic limestones of Florida. Rep. Invest. Florida Geol. Surv., 3: 1–105.

Hutchinson, G. E. 1943. Biogeochemistry of aluminum and certain related elements. Quart. Rev. Biol., 18: 1–29; 128–153; 242–262; 331–363.

——— 1950. The biogeochemistry of vertebrate excretion. Bull. Amer. Mus. Nat. Hist., 96: 1–554.

Hutchinson, G. E., and Anne Wollack. 1943. Biological accumulators of aluminum. Trans. Conn. Acad. Arts Sci., 35: 75–127.

Hutchinson, G. E., J. K. Setlow, and J. L. Brooks. 1946. Biochemical observations on *Asterias forbesi*. Bull. Bingham Oceanogr. Coll., 9(13): 3–6.

Hutchinson, G. E., A. Wollack, and J. K. Setlow. 1943. The chemistry of lake sediments from Indian Tibet. Amer. J. Sci., 241: 533–542.

Ichikawa, R., and Y. Hiyana. 1956. Deposition of radiostrontium in the various tissues of jack mackerel, mackerel, and tuna. *In* Research on the Effects and Influences of the Nuclear Bomb Test Explosions. Ueno, Tokyo, Japan Society for the Promotion of Science, pp. 1143–1150.

Iddings, J. P., and E. W. Morley. 1915. Contributions to the petrography of Java and Celebes. J. Geol., 23: 231–245.

Imbrie, John. 1955. Quantitative Lithofacies and Biofacies Study of Florena Shale (Permian) of Kansas. Bull. Amer. Assn. Petrol. Geol., 39: 649–670.

Jacob, K. D., W. L. Hill, H. L. Marshall, and D. S. Reynolds. 1933. The composition and distribution of phosphate rock with special reference to the United States. Tech. Bull. U. S. Dep. Agric., 364: 1–89.

Jacobson, Louis, and R. Overstreet. 1947. A study of the mechanism of ion absorption by plant roots using radioactive elements. Amer. J. Bot., 34: 415–420.

Jackson, M. L., S. A. Tyler, A. L. Willis, G. A. Bourbeau. R. P. Pennington. 1948. Weathering sequence of clay size minerals in soils and sediments. J. Phys. Coll. Chem. 52: 1237–1260.

Jayaraman, W. 1940. Origin of celestine in the Cretaceous beds of Trichy. Quart. J. Indian Inst. Sci., 3: 25–27.

Jolibois, P., and C. Hebert. 1946. Sur la composition chimique des phosphates de calcium naturels. C. R. Acad. Sci., Paris, 222: 569–572.

Joseph, N. R. 1939. Interaction of amino acids and salts. III. The determination of the activities of calcium, barium and strontium chloride in amino acid solutions by means of electrodes of the third kind. J. Biol. Chem., 130: 203–217.

Katchenkov, S. M. 1948. Elementary composition of petroleum ashes. C. R. Acad. Sci. U.R.S.S., 62: 361–363.

——— 1949. Correlation of petroleum by the microelements. C. R. Acad. Sci. U.R.S.S., 67: 503–505.

——— 1952. Characteristics of the lower Permian sediments with chemical element distribution, determined by spectral analysis. C. R. Acad. Sci. U.R.S.S., 82: 961–994.

Kinney, E. M., and E. V. McCollum. 1923a. A study of the rate of deposition and of patterns of absorption of strontium in the rat. J. Pharmacol., 21: 165–176.

———— 1923b. Untersuchungen űber die Geschwindigkeit der Ablagerung und die Aufnahmewege von Strontium bei Ratten. Ber. Ges. Physiol., 20: 297.

Knopf, A. 1917. Strontianite deposits near Barstow, California. Bull. U. S. Geol. Surv., 660: 257–276.

Kohlrausch, F., and F. Rose. 1893. Die Löslichkeit einiger schwer lőslicher Körper im Wasser, beurteilt aur der elektrischen Leitungsfähigkeit der Lösungen. Z. Phys. Chem., 12: 234–243.

Konig, J. 1874. Substitution des Kalkes in den Knochen, und Einfluss kalkarmer Nahrung auf die Zusammensetzung der Knochen. Landw. Jb., 3: 421–435.

Knauss, H. J. and J. W. Porter. 1954. The absorption of inorganic ions by Chlorella pyrenoidosa. Plant Physiol., 29: 229–234.

Kraus, E. H. 1904. Occurrence and distribution of celestite near Syracuse, New York, and its relation to the vermicular limestones of the salina epoch. Amer. J. Sci., ser. 4, 18: 30–39.

Krogh, A. 1946. The active and passive exchanges of inorganic ions through the surfaces of living cells and through living membranes generally. Proc. Roy. Soc. London, Ser. B, 133: 140–200.

Kulp, J. L., W. R. Eckelmann, A. R. Schulert. 1957. Strontium-90 in Man. Science, 125(3241) : 219–225.

Kulp, J. L., K. Turekian and D. W. Boyd. 1952. Strontium content of limestones and fossils. Bull. Geol. Soc. Amer., 63: 701–716.

Lacroix, A. 1922. Mineralogie de Madagascar: Paris. Vol. 2, 469 pp.

Landes, K. K. 1929. The strontium occurrence near La Conner, Washington. Amer. Min., 14: 408–413.

Landergren, Sture. 1943. Geokemiska studier över Grängesbergsfaltets järnmalmer. Ingen. Vetensk. Akad. Handl., 172: 1–72.

Larsen, E. S., M. H. Fletcher and E. A. Cisney. 1952. Strontian apatite. Amer. Min., 37: 656–658.

Laspeyres, H., and E. Kaiser. 1897. Mitteilungen aus dem mineralogische Museum der Universität-Bonn. Z. Krystallogr., 27: 41–59.

Lewin, S. Z., P. J. Lucchesi, and J. E. Vance. 1953. Significance of fungus growth in analytical and radiochemical work with strontium-containing solutions. J. Amer. Chem. Soc., 75: 6058.

Linck, G. 1926. Cőlestin pseudemorph nach Fasergips nebst einem Anhang uber Tutenmergel. Chem. D. Erde, 2: 481–488.

Lopez De Azcona, I. M., and A. C. Pulg. 1947a. Trace elements in Asturian coal ashes. Bol. Inst. Geol. Fsp., 60: 3–9.

————1947b. Spectrochemical analysis of ash from Asturian coal. An. Fisica Quimica, 43: 48–50.

Lowenhaupt, B. 1956. The transport of calcium and other cations in submersed aquatic plants. Biol. Rev., 31: 371–395.

Lowenstam, H. A. 1954a. Environmental relations of modification compositions of certain carbonate secreting marine invertebrates. Proc. Nat. Acad. Sci., Wash., 40: 39–48.

———— 1954b. Factors affecting the aragonite-calcite ratios in carbonate secreting marine organisms. J. Geol., 62: 284–322.

———— 1955. Aragonite needles secreted by algae and some sedimentary implications. J. of Sediment. Petrol., 25: 270–272.

Lundegardh, H. G. 1929–1934. Die quantitative Spektralanalyse der Elemente. Jena, G. Fischer, 2 vols.

Lundegardh, H., and H. Bergstrand. 1940. Spectral-analytical investigations into the content of mineral substances in the liver. Nova Acta Soc. Sci. Upsal., 12: 1–46.

McCance, R. A., and J. M. Masters. 1938. The chemical composition and acid-base balance of *Archidoris britannica*. J. Mar. Biol. Assn. U. K., 22: 273–279.

MacDonald, N. S., R. E. Nusbaum, R. Stearns, F. Ezmirlian, C. McArthur, and P. Spain. 1951. The skeletal deposition of non radioactive strontium. J. Biol. Chem., 188: 137–143.

MacGregor, A. M. 1930. The geology of the country between Gatomma and Battlefields. Bull. Geol. Surv. S. Rhod., 17: 1–144.

Marshall, H. L., K. D. Jacob, and D. S. Reynolds. 1932. Occurrence of fluorine in natural phosphates. Industr. Engng. Chem. (Anal.), 24: 86–89.

Matz, K. B. 1944. Celestite from the magnesite deposits of Oberdorf on the Lamming, Upper Styria. Neues Jb. Miner., Mh. (1944) : 245–250.

Mayer, F. K. 1931. Röntgenographische Untersuchungen űber die modifikationen des Kalziumkarbonates in Gastropodenschalen. Chem. D. Erde. 6: 239–252.

Mayer, F. and E. Weineck. 1932. Die Verbreitung der Kalziumkarbonates im Tierreich, unter besonder Berűcksichtigung der Wirbellosen. Jena. Z. Med. Naturw., 66: 199–221.

Mazia. D. 1938a. The binding of calcium, strontium, and barium by *Elodea* protoplasm. J. Cell. Comp. Physiol., 11: 193–203.

———— 1938b. Cation exchange in *Elodea*. J. Cell. Comp. Physiol., 11: 455–463.

———— 1940. The binding of ions by cell surface. In Cold Spr. Harb. Symp. Quant. Biol., 8: 195–203.

Mellor, J. W. 1923. The alkaline earths. In A Comprehensive Treatise on Inorganic and Theoretical Chemistry. London, Longmans Green and Co., 3: 619–908.

Menzel, R. G. 1954. Competitive uptake by plants of potassium, rubidium, cesium and calcium, strontium and barium from soils. Soil Sci., 77: 419–425.

Miyake, K. 1914. Influence of the salts common in alkali soils upon the growth of rice plant. Bot. Mag., Tokyo, 28: 1–4.

Molisch, H. 1923. Mikrochemie Der Pflanze. Jena, G. Fischer, pp. 1–434.

Monaghan, P. H., and M. L. Lytle. 1956. The origin of calcareous oolith. Jour. Sediment. Petrol., 26: 111–118.

Morse, H. W., and J. D. H. Donnay. 1932. Optics and structure of three dimensional spherulites. Amer. Min., 21: 201–202; 391–426.

Mugge, O. 1899. Über Pseudomorphosen von Cölestinnach Fasergyps. Neues Jb. Min. Geol. Paläont., pt. 2 (1899): 187–188.

Muller, H. 1858. Über die Thallasicollen, Polycystinen und Acanthometrendes Mittelmeeres. Abh. Dtsch. Akad. Wiss. Berl., (1858): 1–62.

Nishita, H., B. W. Kowalewsky, and K. H. Larson. 1956a. The influence of soil organic matter on mineral uptake by barley plants. Soil Sci., 82: 307–318.

Nishita, H., B. W. Kowalewsky, A. J. Steen, and K. H. Larson, 1956b. Fixation and extractability of fission products contaminating various soils and clays. I. Sr90, Y91, Ru106, Cc137, and Ce144. Soil Sci., 81: 317–326.

Noddack, I., and W. Noddack. 1934. Herkunftsuntersuchungen. Angew. Chem., 47: 637–641.

Noll, W. 1931a. Über die geochemische Rolle der Sorption. Chem. D. Erde 6: 552–577.

————. 1931b. Über die Bestimmung des Strontiums in der Mineral-und Gestein-analyse. Z. Anorg. Chem., 199: 193–208.

————. 1934. Geochemie des Strontiums. Mit Bemerkungen zur Geochemie des Bariums. Chem. D. Erde, 8: 507–600.

Oakley, K. P., and C. R. Hoskins. 1950. New evidence on the antiquity of Piltdown man. Nature, Lond., 165: 379–382.

Odum, H. T. 1950a. Strontium biogeochemistry, ecosystems and paleoecological tools. Report of the committee on a treatise on Marine ecology and paleoecology, National Research Council, Washington, D. C., 10: 55–58.

————. 1950b. The biogeochemistry of strontium. Yale University, unpublished Thesis, pp. 1–373.

————. 1951a. The stability of the world strontium cycle. Science, 114 (2964): 407–411.

————. 1951b. Notes on the strontium content of sea water, celestite radiolaria, and strontianite snail shells. Science, 114: 211–213.

————. 1951c. Nudibranch spicules made of amorphous calcium carbonate. Science, 114: 395.

————. 1957. Strontium in natural waters. Publications of the Institute of Marine Science, 4: 22–37.

Odum, H. T., and E. P. Odum. 1955 Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol. Monogr., 25: 291–320.

Okamoto, Y. 1943. Minerals of Beppu, Oita Prefecture. Tech. Repts. Kyushu Imp. Univ., 18: 231–241.

Papillon, F. 1870. Recherches experimentales sur les modifications de la composition immediate des os., C. R. Acad. Sci., Paris, 71: 372–374.

Payne, J. H. 1946. A study of the chemical alteration of basalt in the Kilauea Region of Hawaii. J. Geol., 54: 345–358.

Pecher, C. 1941. Biological investigations with radioactive calcium and strontium. Proc. Soc. Exp. Biol. Med., 46: 86–91.

Pecora, W. T. 1942. Nepheline syenite pegmatites, Rocky Boy Stock, Bearpaw Mountains, Montana. Amer. Min., 27: 397–424.

Pirschle, K. 1934. Comparative investigations on the physiological effect of the elements as shown by growth experiments with *Aspergillus niger*. Planta, 23: 177–224.

Pitkovska, T. N. 1939. Strontium and barium in the cap rocks of Romny and Isachkov salt domes. J. Geol. (Acad. Sci. Ukraine SSR, Inst. Geol.), 6: 91–93.

Posnak, E. 1940. Deposition of calcium sulfate from sea water. Amer. J. Sci., 238: 559.

Potapenko, G. 1925. Ueber die Spektralanalyse mit Teslaströmen und mit ungedompften Schwingungen. Trud. Nauch.-issled. Inst. Fiz. Kristall., Moscow, 3: 16.

Prenant, M. 1928. Contributions a l'etude cytologique du calcaire. IV. La vaterite chez les animaux. Bull. Biol., 62: 21–50.

Rafter, T. A. 1945. Boron and strontium in New Zealand coal ashes. Nature, 155: 332.

Ramage, H. 1936. Biological distribution of metals. Nature, Lond., 137: 67.

Ramsey, J. C., and F. H. Heath. 1950. Mineral Analyses of salt water sponges of Florida. Unpublished paper presented at Fla. Acad. of Science in 1950.

Rankama, K. 1946. On the geochemical differentiation in the earth's crust. Bull. Comm. Geol. Finl., 24 (137): 1–39.

————. 1954. Isotope Geology. New York, McGraw-Hill, pp. 1–535.

Rankama, Kalervo, and T. G. Sahama. 1950. Geochemistry. Chicago, University of Chicago Press, pp. 1–911.

Rediske, J. H., and A. A. Selders. 1953. Absorption and translocation of strontium by plants. Plant Physiol., 28: 594–605.

Revelle, R., and K. O. Emery. 1951. Barite concretions from the ocean floor. Bull. Geol. Soc. Amer., 62: 707–724.

Reynolds, D. S., K. D. Jacob, and W. L. Hill. 1929. Ratio of fluorine to phosphoric acid in phosphate rock. Industr. Engng. Chem., (Aanal.), 21: 1253–1256.

Reynolds, F. M. 1948. Occurrence of vanadium, chromium and other unusual elements in certain coals. J. Soc. Chem. Ind. Lond., 67: 341–345.

Rice, T. R. 1956. The accumulation and exchange of strontium by marine planktonic algae. Limnolog. and Oceanog., 1: 123–138.

Robinson, W. O. 1914. The inorganic composition of some important American soils. Bull. U. S. Dept. Agr., 122: 1–27.

Robinson, W., L. Steinkoenig, and C. F. Miller. 1917. The relation of some of the rarer elements in soils and plants. Bull. U. S. Dept. Agr., 600: 1–25.

Robison, R., and T. H. Rosenheim. 1934. Calcification of hypertrophic cartilage *in vitro*. Biochem. J., 28: 684–698.

Robison, R., K. A. O'Dell Law, and A. H. Rosenheim. 1936. Deposition of strontium salts in hypertrophic cartilage *in vitro*. Biochem. J., 30: 66–68.

Rogers, L. H., O. E. Gall, L. W. Gaddum, and R. M. Barnette. 1939. Distribution of macro and micro elements in some soils of peninsular Florida. Bull. Fla. Agric. Exp. Sta., 341: 1–31.

Rogers, R. F. 1924. Mineralogy and petrology of fossil bone. Bull. Geol. Soc. Amer., 35: 535–556.

Romney, E. V., W. A. Rhoads, and K. Larson. 1954. Plant uptake of strontium 90, ruthenium 106, cesium 137, and cerium 144 from three different types of soil. U. S. Atomic Energy Comm. University of California, Los Angeles, No. UCLA-294: 1–28.

Rusoff, L. L. 1941. Distribution of trace elements in the newborn calf as influenced by the nutrition of the dam. Bull. Fla. Agric. Exp. Sta., 359: 1–48.

Rusoff, L. L., and L. W. Gaddum. 1938. The trace element content of the newborn rat (as determined spectrographically). J. Nutr., 15: 169–176.

Rusoff, L. L., L. H. Rogers, and L. W. Gaddum. 1937. Quantitative determination of copper and estimation of other trace elements by spectrographic methods in wire grasses from "salt sick" and healthy areas. J. Agric. Res., 55: 731–738.

Sahama, T. G. 1945a. Spurenelemente der Gesteine im südlichen Finnisch-Lappland. Bull. Comm. Geol. Finl., 23 (135) : 1–86.

Sahama, T. G. 1945b. On the chemistry of the east Fennoscandian Rapakivi granites. Bull. Comm. Geol. Finl., 24 (136) : 15–67.

Samoilov, J. V. 1917. Paleophysiology: the organic origin of some minerals in sedimentary rocks. Miner. Mag., 18: 87–98.

————. 1922. Palaophysiologie und ihre geologische Bedeutung. Mber. Dtsch. Geol. Ges., 7: 227–244.

Schewiakoff, W. 1902. Beitrage zur kenntnis der Radiolarian Acanthometra. Mem. Acad. Imp. Sci. St. Petersb., Ser. 12, 10: 1–40.

————. 1926. Monografia: Acantharia. Fauna e Flora del Golfo di Napoli, 37: 1–755.

Schmidt, W. J. 1944. Zur Optic der Spicula von Doris. Z. Morph. Ökol. Tiere, 40: 389–405.

Severin, I. 1932. La preuve de la mort par submersion suivant qu'elle a eu lieu dans une riviere ou dans la mer. Rev. Path. Comp., 32: 559–571.

Shimer, J. A. 1943. Spectrographic analysis of New England granites and pegmatites. Bull. Geol. Soc. Amer., 54: 1049–1066.

Shreve, R. N., and C. H. Watkins. 1939. New method for strontium nitrate and chloride. Industr. Engng. Chem., (Anal.), 31: 1173–1178.

Skeats, E. W. 1918. The formation of dolomite and its bearing on the coral reef problem. Amer. J. Sci. Ser. 4, 45: 185–200.

Smith, W. W., and T. Tait. 1934. The atomic weight of the calcium contained in very old potassium-rich minerals occurring at Partsoy, Banffshire and at Cape Wrath, Sutherlandshire. Proc. Roy. Soc. Edinb., 54: 88–101.

Spezia, G. 1895. Über den Ursprung des Schwefels in der Schwefelformation von Sizilien. Z. Kristallogr., 24: 412–414.

Spinks, J. W. T., E. Cumming, R. L. B. Irwin, and T. J. Arnason. 1948. Lethal effect of absorbed radioisotopes on plants. Canad. J. Res., 26C: 249–262.

Spooner, G. M. 1949. Observations on the absorption of radioactive strontium and yttrium by marine algae. J. Mar. Biol. Ass. U. K., 28: 587–625.

Steinberg, R. A. 1948. Essentiality of calcium in the nutrition of fungi. Science, 107: 423.

Stoddart, W. W. 1876. On the occurrence of celestine in the Keuper Marls and its influence on the composition of plants. Miner. Mag., 1: 4–7.

Stoeltzner, H. 1908. Über den Einfluss von Strontiumverfutterung auf die chemische Zusammensetzung des wochsenden Knochens. Biochem. Z., 12: 119–137.

Stolkowski, J. 1948. Quelques precisions sur l'analyse quantitative par les rayons X de melanges binaires et ternaires de carbonate de calcium anhydre. C. R. Acad. Sci., Paris, 226: 933–934.

Stout, Wilber. 1941. Dolomites and limestones of western Ohio. Bull. Geol. Surv. Ohio, ser. 4, 42: 1–468.

Sugehire, Y., S. Yoshine, Y. Tsukamoto, M. Akamatsu, K. Takahashi and T. Mori. 1956. Transmission and metabolism of strontium 90 in aquatic animals. In research on the Effects and Influences of the Nuclear Bomb Test Explosions. Ueno, Tokyo, Japan Society for the Promotion of Science, pp. 1135–1142.

Sverdrup, H. U., M. W. Johnson, and R. H. Fleming. 1942. The Oceans, Their Physics, Chemistry and General Biology. New York, Prentice-Hall, 1–1087.

Sulze, W. 1942. Über die physiologische Bedeutung des Kalksackchenapparates der Amphibien. Pflüg. Arch. Ges. Physiol., 246: 250–257.

Swan, E. F. 1956. The meaning of strontium-calcium ratios. Deep Sea Res., 4: 71.

Tate, F. G. H., and H. K. Whalley. 1940. The spectrographic analysis of tobacco ash. Analyst., 65: 587–593.

Taylor, J. H. 1950. Baryte-bearing nodules from the middle Lias of the English east Midlands. Miner. Mag., 29 (208): 18–26.

Thilo, E. 1934. Über die Resultate der Analysen zweier Kohlenaschen. Z. Anorg. Chem., 218: 201–209.

Thompson, T. G., and T. J. Chow. 1955. The strontium-calcium atom ratio in carbonate-secreting marine organisms. In Papers in Marine Biology and Oceanography, Supplement to Deep-Sea Research, 3: 30–39.

Thompson, T. G., and R. J. Robinson. 1932. Chemistry of the sea. in vol. 5, Oceanography in Physics of the Earth. Bull. Natl. Res. Coun., Wash., 85: 95–203.

Thomson, Thomas. 1836. Description and analysis of emmonite, a new species of carbonated strontian from America. Rec. Gen. Sci., 3: 415–417.

Toropov, W. A., and P. F. Konovalov. 1943. Solid solutions of calcium and strontium orthosilicates. C. R. (Doklady) Acad. Sci. U.R.S.S., 40: 155–157.

Trueman, E. R. 1942. The structure and deposition of the shell of *Tellina tenuis*. J. R. Micr. Soc., 62: 69–92.

———. 1944. Occurrence of strontium in molluscan shells. Nature, Lond., 153: 142.

Turekian, K. 1955. Paleoecological significance of the strontium-calcium ratio in fossils and sediments. Bull. Geol. Soc. Amer., 66: 155–158.

Turekian, K., and H. W. Feely. 1956. Variations in the abundance of trace elements in a eupelagic Atlantic core (Abstact). Bull. Geol. Soc. Amer., 67:1739.

Turekian, K., and J. L. Kulp. 1956. The geochemistry of strontium. Geochim. et Cosmoch. Acta, 10: 245–206.

Tsuchiya, Yasuhiko. 1944. Distribution of strontium in calcareous organisms. I. Strontium content of reef forming corals. J. Agr. Chem. Soc. Japan, 20: 653–654.

———. 1948. Studies on the method for the preparation of strontium from corals and calcareous algae. J. Fac. Agr., Kyushu Univ., 9: 65–68.

Tyndale-Biscoe, R. 1931. The geology of the country around Shamva, Mazoe District. Bull. Geol. Surv. S. Rhod., 18: 1–87.

Van Tongeren, W. 1938. Contributions to the knowledge of the chemical composition of the earth's crust in the East Indian Archipelago. I. The spectrographic determination of the elements according to the arc methods in the Range 3600–5000 Angstroms on the occurrence of the rarer elements in the Netherlands East Indies. Amsterdam, D. B. Centen's Uitgevers-Maat-Schappij N. V.

Vaughan, J., M. Tutt and B. Kidman. 1952. Haddow, A. Biological Hazards and Atomic Energy. Oxford, Clarendon Press, pp. 145–170.

Vinogradov, A. P. 1938. Geochemistry and Biochemistry. Uspek. Khim., 7: 639–686.

———. 1945. To the chemical study of the biosphere. Pedology, 7: 348–354.

Vinogradov, A. P., and T. F. Borovik-Romanova. 1945. On the geochemistry of strontium. C. R. (Doklady) Acad. Sci. U.R.S.S., 46: 193–196.

Wager, L. R., and R. L. Mitchell. 1943. Preliminary observations on the distribution of trace elements in the rocks of the Skaergaard intrusion, Greenland. Miner. Mag., 26: 283–296.

———. 1951. The distribution of trace elements during strong fractionation of basic magma, a further study of the Skaergaard intrusion, East Greenland. Geochim. et Cosmoch. Acta, 1: 129–208.

Walsh, T. 1945a. Effect produced on the growth of plants by substitution of strontium for calcium in acid soils. Chemie and Industrie, 56: 494.

————. 1945b. The effect on plant growth of substitution of strontium for calcium in acid soils. Proc. R. Irish Acad., 50B: 287–294.

Wassermann, A. 1948. Adsorption of calcium ions by acid extracted brown alga under continuous flow conditions. Nature, Lond., 161: 562.

Wattenberg, H., and E. Timmermann. 1938. Die Löslichkeit von Magnesiumkarbonat und Strontiumkarbonat in Seewasser. Kieler Meeresforsch., 2: 81–94.

Webb, D. A., and W. R. Fearon. 1937a. Studies on the ultimate composition of biological material. I. Aims, scope, and methods. Sci. Proc. R. Dublin Soc., 21: 487–504.

Webb, D. A. 1937b. Studies on the ultimate composition of biological material. Pt. II. Spectrographic analyses of marine invertebrates with special reference to the chemical composition of their environment. Sci. Proc. R. Dublin Soc., 21: 505–539.

————. 1938. Strontium in sea water and its effect in calcium determinations. Nature, Lond., 142: 751–752.

Wheeler, W. P. 1919. Studies relating to calcium metabolism. Bull. N. Y. St. Agric. Exp. Sta., 468: 1–43.

Wiklander, L. 1946. Studies on ionic exchange with special reference to the conditions in soils. K. Lantbruks Högskol. Ann., 14: 1–171.

Wilson, S. H. 1941. Note on spectrographic analysis as a means of testing for sea-water damage on metals. J. Soc. Chem. Indus., Trans., 60: 286–288.

Wilson, S. H., and M. M. Fields. 1942. Studies in spectrographic analysis. II. Minor elements in a seaweed *(Macrocystis pyrifera)*. N. Z. J. Sci. Tech., 23: 47–48.

Wolf, A. G. 1926. Big Hill Salt Dome, Matagorda County, Texas. in DeGolyer et al. Geology of Salt Dome Oil Fields. Chicago, University of Chicago Press, pp. 691–717.

Wolfmann, J. 1896. Studium uber die Loslichkeitsverhaltnisse einiger Strontiumsalze, besonders des Strontiumsulfates. Österr.-Ungar. Zeitschr. Zuckerindus., 25: 986–997.

Young, R. S. 1935. Certain rarer elements in soil and fertilizer and their role in plant growth. Mem. Cornell Agric. Exp. Sta., Memoir, 174: 1–70.

Zeller, E. J., and John L. Wray. 1956. Factors influencing precipitation of calcium carbonate. Bull. Amer. Ass. Petrol. Geol., 40: 140–152.

Metabolism of a Laboratory Stream Microcosm[1]

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Introduction

THE MICROCOSM METHOD

Wherever the energy of the sun is being absorbed on earth, living organisms use it to develop complex associations capable of survival. In order to compete, such complexes must recirculate the chemical raw materials making use of whatever physical processes are at hand. Food must be passed from producer to consumer, and the chemicals passed from regenerating consumer back to primary producer. Sometimes there is only molecular diffusion; at other times there are available strong turbulent mechanisms for exchanging substances as effectively as in the blood circulatory systems within organisms. The term ecosystem has been used for the combination of communities of organisms and their circulation systems. Understanding the ecosystem is a main objective of ecology. Unfortunately, most ecosystems in nature are large and consequently difficult to manipulate.

Smaller systems could be handled experimentally. A microscosm is by definition a miniature system. To quote Webster's dictionary it is a "small community, a little world." It seems a logical methodology to study experimental microcosms as a means of understanding the larger macrocosms.

It is also conceivable that study of microcosms can lead to the invention of new ecosystems not present in nature. Perhaps such ecosystems can be developed to maintain themselves by internal ecological mechanisms to man's benefit. The microcosm therefore may be an approach to *community engineering,* one of the bright possibilities for man after his fossil power is gone.

Whereas most kinds of experiments involve isolating a part of a system for study, a microcosm experiment is designed to retain as much of the total complexity as possible, including especially the producer, consumer-regenerator, and circulating phases. This paper is a report on the behavior of a laboratory stream microcosm and the inferences that might be drawn from it about larger flowing systems in nature.

PROBLEMS IN STREAM ECOLOGY

In previously reported studies on natural flowing systems some perplexing issues and hypotheses have been proposed and discussed to account for the patterns of biota and metabolism known to occur in streams. Some of these questions are as follows:

1. *Are stream communities more productive than other aquatic communities* as suggested by data summarized previously (Odum, 1956a) ? If true on the average, does the current modify production because of the circulation per se within the community as well as by bringing fresh media and requirements from outside of the community? Gessner (1937, 1955) has shown that single vascular water plants metabolize more rapidly in circulation. Fox, Simmonds, and Washburn (1935) have described the high metabolism of current adapted animals. Does a current also increase the metabolism of communities isolated in steady state? Do the metabolic rates of ecosystems, which have both photo-synthetic aufwuchs and respiratory slimes change with the current?

2. *Is the metabolism of an adapted steady state community proportional to current velocity at which it grows?* Does the metabolism of an aufwuchs-slime community in adjustment to one current velocity change if the current velocity is changed? These

questions need solution to allow an understanding of metabolism in streams. Are the variations in flow in streams accompanied by variations in metabolism? Is the predominance of aufwuchs in rapids an indication that metabolism is greatest there?

3. *Can an aufwuchs-slime community concentrate and store inorganic nutrients* from passing water as plankton cultures do? Can aufwuchs-slime communities concentrate and store *organic nutrients* from dilute flowing waters for future metabolism as an energy source? Sargent and Austin (1949, 1954) reported some results which suggested that coral reefs might have the ability to extract organic stuff from dilute concentrations in tropical ocean water. Some perpelexing decreases in biochemical oxygen demand in Silver Springs (Odum, 1957) could be similarly interpreted.

Following Pütter's hypothesis, much work such as that of Bond (1933) showed that dilute natural concentrations of dissolved organic matter could not support larger consumer organisms directly under conditions of still water. Bacteria on the other hand were able to grow in dilute media or on surfaces adjacent to media with low organic concentrations (Zobell and Anderson, 1936). Presumably low nutrient media under flowing conditions can also support bacteria on surfaces. The possibility of larger consumers deriving energy from dilute organic matter concentrations flowing past the organisms has not been eliminated. If true for sessile consumers the possibility that it could be true for plankton organisms might be reconsidered for turbulent water. That dissolved organic matter concentrations are maintained at such low levels in the ocean suggests continual metabolic use by plants, animals, or bacteria.

4. *What is the course of metabolism and holistic community structure during succession and climax?* Butcher (1940, 1945, 1947, 1949) and others have described patterns of brief succession and climax in stream communities. The types and kinds of final states have seemed to be infinitely numerous under different hydrographic conditions. What measures of total community structure and function in common among these taxonomically diverse steady states can be observed in a microcosm?

5. *What is a design for a flowing respirometer for attached stream cultures?* What conditions are necessary to produce a typical periphyton (aufwuchs) in place of a plankton type community? Can such communities be cultured at will under controlled conditions? L. Whitford has recently cultured a single species of stream algae in an open circulating trough (personal communication).

Stream Microcosm Apparatus

After a number of trials and failures an apparatus was finally evolved which yielded aufwuchs communities readily and which permitted continual metabolic measurements. In Figure 1 is the microcosm as finally modified. As always, the authors regret that hindsights were not foresights.

A pump circulates water in a closed circuit through the inner tube of a condenser illuminated by four 150 watt R-40 General Electric photo-flood lights. All other tubing is covered with aluminum foil and is in the dark. The temperature is regulated by flow of tap water in the condenser jacket. The temperature is indicated by a thermistor and bridge. While the community is developing and while measurements are not being made, the water is passed through an aerator tank where a flow of air bubbles maintains a constant oxygen and carbon dioxide-bicarbonate condition. Thus all experiments receive the same constant carbon dioxide pressure of the natural air. Because of the continual introduction from the outside, no shortage of carbon dioxide can develop. Carbon dioxide can control rates by its concentration but can never be limiting in the sense of becoming unavailable. A tube from a resevoir carbuoy permits renewal and replacement of medium which is removed for analysis or which evaporates in the aerator. Measurements of the water properties are made by drawing samples from a tap. At times a glass wool filter is used to catch pseudoplankton and make chances of plugging in the smaller tubes less likely.

When metabolic rates are measured, water is routed through a different route so as to bypass the aerator (See Figure 1). After ten minutes of circulation to permit mixing, two 5 cc oxygen samples are drawn for Winkler analysis in a syringe. After a metabolic period of an hour duplicate samples are again drawn for analysis. The average volume of the total metabolic system during this period (about 400 ml) is measured from the height of a circular paraffin block in the water resevoir cylinder of the bypass (Figure 1). After these measurements are made, the system is again routed through the aerator where the oxygen concentrations are returned to normal in a few minutes.

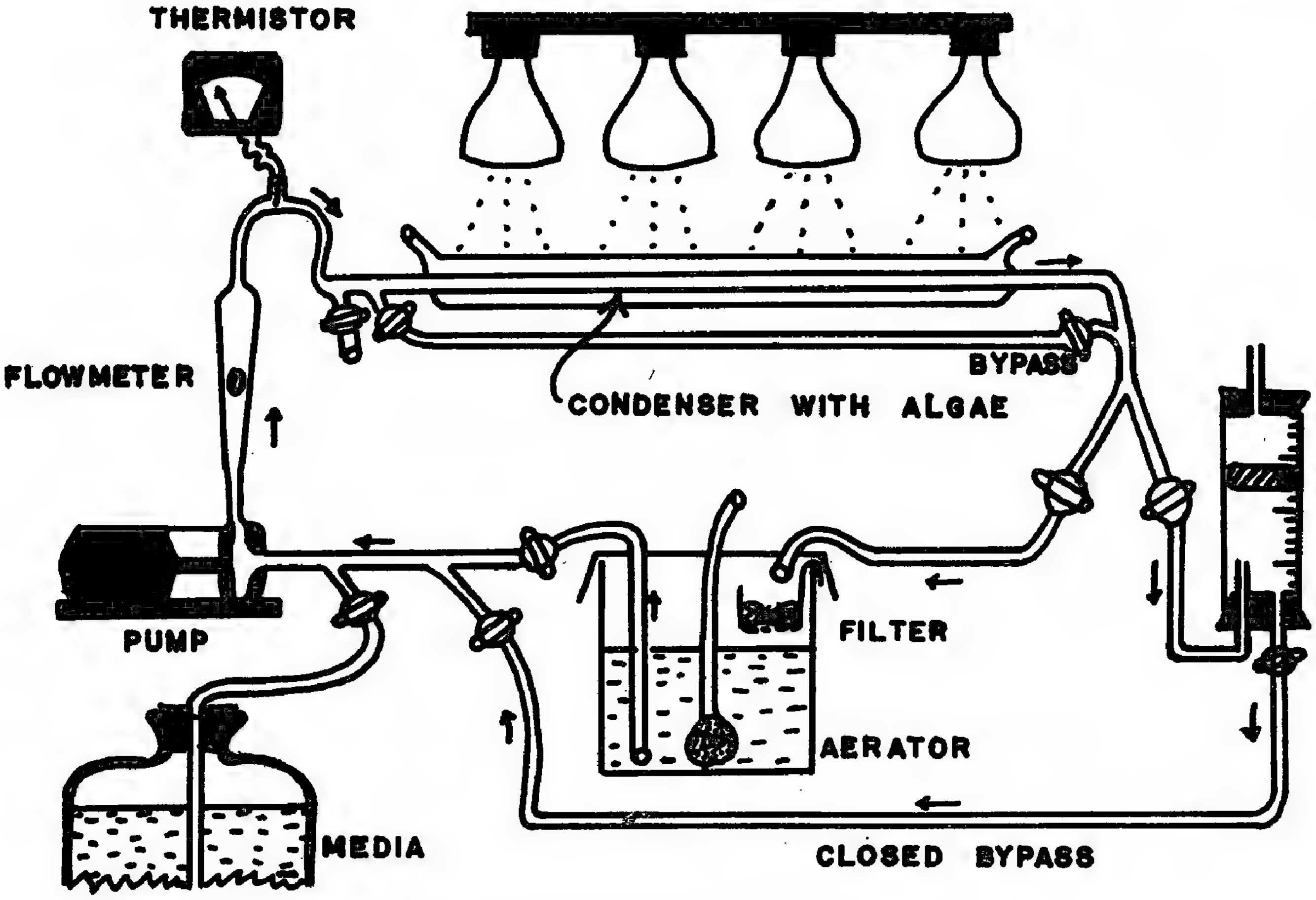

FIG. 1. Flowing microcosm apparatus and respirometer.

A circuit is available to bypass the main photosynthetic community in the condenser also. Current velocities are controlled with a stopcock and indicated by the position of a glass bead in the cone-shaped tube, which after calibration serves as a flowmeter. The pump, Model D–6 produced by Eastern Industries, is a stainless steel centrifugal type powered by a 1/30 Hp electric induction motor, which ran continuously for a year without major mishap.

The Winkler analysis in the syringe is rapid and accurate. One 0.05 cc drop each of manganous sulfate, potassium-hydroxide-potassium iodide solution, and sulfuric acid in usual concentrations are placed in cups of a depression slide. These drops are drawn into the syringe containing the 5 cc water sample in the usual sequence. The clear iodine-containing solution is titrated with a 0.00625N thio-sulfate solution in a bottle. With a fully developed aufwuchs-slime community the oxygen changes for the volume of the system of about 400 cc are as much as 5 mg/l/hr. These large changes in concentration far exceed the variation in values due to analytical error or due to heterogeneity of the waters sampled. No correction was made for oxygen added in reagents.

A considerable effort was made to adapt the gold-zinc electrode used by Ohle (1953) for continuous instantaneous readings of oxygen in the flowing system. These efforts were unsuccessful. It was not possible to obtain readings which could be repeated. Apparently, continuously changing electrode surfaces, attachments of slime, and other current-sensitive effects could not be reproduced. The attempts included washing of electrodes in acid, flushing electrodes with distilled water while not in use, and study of time curves of amperes following closure of electrical circuit. It was apparent during the two months of work with the zinc electrode in the system that only bacteria and fungi were being cultured in thick fuzzy mats. The first success with algae followed the removal of the zinc from the system.

Similar failure to obtain reproducible results in polarographic oxygen measurements in continuous flow systems were recently reported by Ambuhl (1955) and Lynn and Okun (1955).

Where phosphate and nitrate analysis were made to indicate nutrient levels, colorimetric methods were used with a Bausch and Lomb spectronic 20 instrument. The strychnidine method for nitrate (Zwicker and Robinson, 1944) and the ammonium molyddate method for phosphorus were used (Robinson and Thompson, 1948).

A number of the early experiments were terminated after 3 weeks by the slippage of the thick mats of filamentous and gelatinous aufwuchs from the side of the condenser so that the system became plugged. It was not until later experiments that this was prevented by placing a cylindrical layer of plastic window screen within the condenser for the algae to develop on. Thereafter no massive clumps broke loose.

The current velocities were fairly uniform in the condenser tube. Flow of water containing particles showed the observer a fairly laminar flow. For example, when the flow meter indicated an average flow of 0.1 m/sec there was a flow of this magnitude within 2.5 mm. of the wall or less. Although 0.08–0.2 m/sec flow in the free water of streams is not large, a flow of this magnitude within the aufwuchs occurs in nature only when much greater currents are occurring in the free water. Thus 0.08–0.2 m/sec is referred to as a high current velocity subsequently in this discussion.

Sequence of Experiments

From November 1955 to November 1956 manipulations of the stream microcosm were studied. During the course of these experiments the metabolism of the community under light and dark conditions was measured. Except during metabolism measurements the condenser portion of the community was in continuous light 24 hours a day. When respiration rates were measured, black covers were placed over the condenser. Thus the condenser might be described as a flowing light and dark bottle. The oxygen decreases for the system were recorded in mg/hr as respiration and represented by R. The oxygen changes during illumination were considered to be the net production of the community represented by P_n. The oxygen changes of respiration (R) were subtracted algebraically from the oxygen changes during photosynthesis (P_n) to obtain the gross primary production P (photosynthesis).

The sequence of measurements of photosynthesis and respiration through the successive experiments is recorded in the series of graphs in Figues 2–11. Extrapolated lines are dashed. Where photosynthesis of the system was in excess of the respiration of the whole system, the area between the graphs is shaded to indicate net storage of organic matter. Nutrient conditions, the gross color of the community, and other properties of the experiments are described in chronological order.

At no time did any plankton communities develop. The system filtered and removed all pseudoplankton whether the glass wool filter was used or not. No algal blooms ever developed in the water—only on the tube surfaces.

A. SUCCESSION AND METABOLISM FOLLOWING INTRODUCTION OF A READY-FORMED COMMUNITY; HIGH CURRENT VELOCITY (FIGURE 2)

The first success in developing a green aufwuchs followed the introduction of a blade of eel grass and water from Silver Springs, Florida enriched with a commercial inorganic fertilizer mixture (hyponex). For the chemical characteristics of Silver Springs water see Odum (1957). Previously, many introductions of algae, lake waters, and soils had given opportunity for many species to become "seeded." The eel grass blade and its already existing aufwuchs demonstrated a high metabolism from the start which gradually diminished. It was immediately obvious that the initial community was being replaced by succession. This succession passed through a period of rich diatom growth followed by a replacement with blue-green algae. The eel grass showed decomposition indicating release of organic supplements. P and R were about equal but both decreased as the excess nutrient levels diminished (Figure 2). The stimulating effect of the addition of a dilute natural medium is indicated on February 18. Since during January and February neither P nor R was much in excess, the total organic matter originally added had not diminished although the apparent decomposition of the eel grass blade indicated a reworking of the organic matter. The experiment ended when the tubes plugged. The current velocity during these experiments was high, 0.1—0.2 m/sec.

RADIOPHOSPHORUS UPTAKE (FIGURE 2)

On February 16, 1956 10 microcuries of p^{32} as phosphate were added to the aerator reservoir (1 liter). A survey meter showed the immediate localization of the radioactive phosphorus in the walls of the tubes, especially the tygon. After one hour and at intervals, five cc samples were evaporated in nickel planchettes and assayed for radioactivity in a proportional scaler. The community was in light for 6 hours and then put in the dark for 6 hours. The levels were not at any time significantly higher than background. There had been an effective removal of the added phosphorus. The implication of the rapid uptake of the phosphorus by the aufwuchs is that there is a high turnover and flux of phosphorus although the concentrations in the water at any time are extremely small. The total phosphorus concentration in the water was 0.05 mg/l.

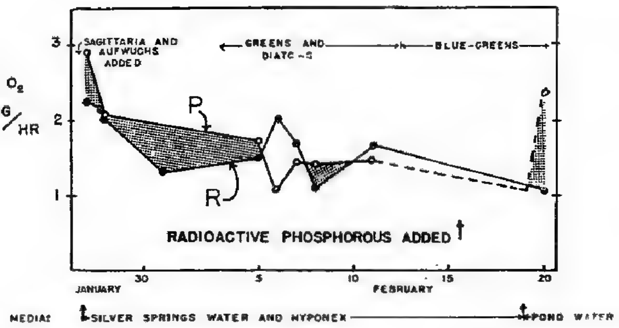

FIG. 2. Succession and metabolism in the microcosm at high current velocity following introduction of water and a ready-formed community.

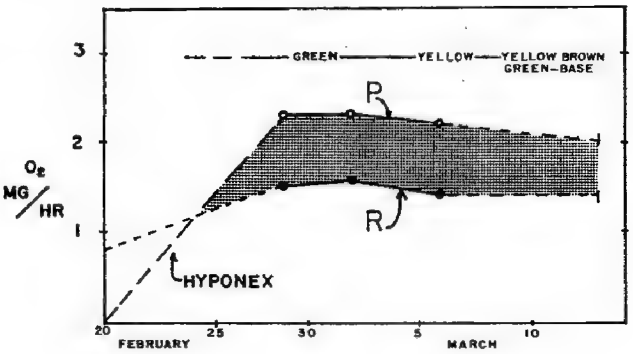

FIG. 3. Growth and succession in a fertilized system at high current velocity.

B. GROWTH AND SUCCESSION IN A FERTILIZED SYSTEM

(FIGURE 3)

On February 20 after the condenser was cleaned out except for small bits of aufwuchs firmly attached in crevices, and an extremely rich inorganic medium was introduced consisting of one gram of hyponex per liter. This system contained far higher concentrations of nutrients than in later experiments and might be compared to the condition initially in fertilized ponds. Within a week a brilliant green aufwuchs developed with a great excess of photosynthesis over respiration meaning that organic matter was being synthesized (Figure 2). No further nutrients were added and as conditions in the recirculating medium changed, the community passed through a succession of color to a brilliant yellow and then orange. There was some green at the upstream end of the community and on the inside of the thick gelatinous mats of algae. Examination of the aufwuchs showed a small blue-green alga almost of bacterial size as dominant. The orange color was due to the small blue greens. Many other blue greens were also present. With the increasing deposits of organic matter, the system finally plugged on March 14.

C. COMMUNITY SUCCESSION WITH LOW NUTRIENT WATER, NUTRIENT-SATURATED SUBSTRATES, AND HIGH CURRENT VELOCITY (FIGURE 4)

After the condenser communities were mostly removed, a low nutrient medium resembling types more often found in nature was introduced. This was a medium described by Rhode quoted in Brunel, Prescott, and Tiffany (1950). Although it was not realized until later, the previous history of the microcosm was important since the films of slime in the dark tubes of the system and in the plastic were holding organic and inorganic nutrients thus affecting the system's metabolism for many days subsequently. Thus this experiment began with a history of 3 months rich growths with ample opportunity for invisible storage of organic matter and nutrients in the walls of the system. Efforts to remove all visible accumulation of organic matter did not reduce this effect appreciably.

With the dilute Rhode medium a community developed less rapidly than with the hyponex but in the subsequent weeks did cover the system and pass through an evolution of color from green to yellow (Figure 4).

Perplexing at first was the fact that photosynthesis did not exceed the respiration of the system during the entire growth period. Here one had a net loss of organic matter of the ecosystem but a regular succession and growth of the visible community. Such metabolic regimes are likely to be common in nature where blooms are observed but where the total P/R is less than 1. Whether the photosynthetic part of the community was deriving heterotrophic energy supplements was not certain but there was ample opportunity for this to have occurred. The aufwuchs slipped and plugged on April 9. The slipping occurred as the older cells touching the glass turned brown.

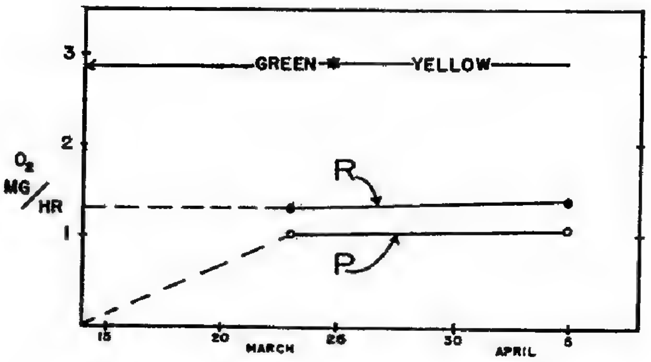

Fig. 4. Community succession with low nutrient water, nutrient-saturated substrates, and high current velocity.

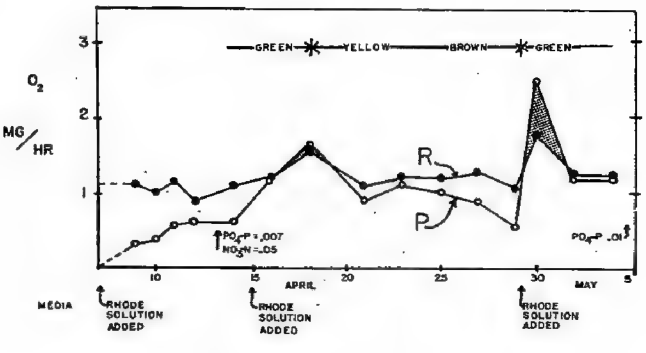

Fig. 5. Bloom pulses in a nutrient-starved steady state community adapted to high current velocities.

D. BLOOM PULSES IN A NUTRIENT-STARVED STEADY STATE COMMUNITY ADAPTED TO HIGH CURRENT VELOCITIES

(FIGURE 5)

After the deposits of the system were cleaned out and new media added, the succession and trends followed a new growth sequence similar to that previously described. As the condenser surfaces became covered with algae, the community became green and and photosynthesis increased indicating that there was net plant production and growth. However, in the total system, respiration (R) was generally in excess of photosynthesis (P, Figure 5). Although there was an obvious growth of the photosynthetic part of the community, the inorganic nutrient levels (nitrate and phosphate) were low resembling the conditions for growths that often occur in natural systems. The succession of color of aufwuchs from green to yellow was reversible. When additional new medium was added to replace that drawn off during measurements, a pulse in photosynthesis and respiration occurred with a return to the green color. As in previous sequences these was a tendency for the metabolic rate curves to level off with metabolism of both photosynthesis and respiration at about 1 mg/hr for the whole microcosm. A somewhat peculiar characteristic of the system was the tendency for low photosynthesis that occurred when the total volume of the system became low on April 13 and again on April 29. Although the nutrient levels in the water were insignificant compared to those found in the aufwuchs-slimes, the decrease of circulating volume affected the ratio of P and R. On May 4 the aufwuchs again slipped and plugged the system just after its bloom condition.

E. COMMUNITY SUCCESSION AND STEADY STATE ADJUSTMENT TO LOW CURRENT VELOCITIES (FIGURE 6)

Again the system was cleaned except for a few spots to act as a "seed" to provide the same possible populations. Whereas the four previous sequences had been studied under conditions of high current velocity (0.09–0.21 m/sec), the next sequence beginning on May 5 (Figure 6) was studied under conditions of low current velocity (0.02 m/sec) with the same dilute inorganic medium and with the same "seeding technique." It was reasoned that the effect of current velocity on steady state adjustments might be determined.

The sequence of events was remarkably similar with a rapid growth of the green aufwuchs over the surfaces of the condenser tube and a development of a large photosynthetic and respiratory metabolism. After the peak of the activity the community again turned yellow as the metabolism adjusted to lower steady state levels of P and R.

The principal difference between this sequence and the ones at high velocity was the lower initial respiratory rate prior to the algal bloom and lower metabolic rates after the steady state began to develop.

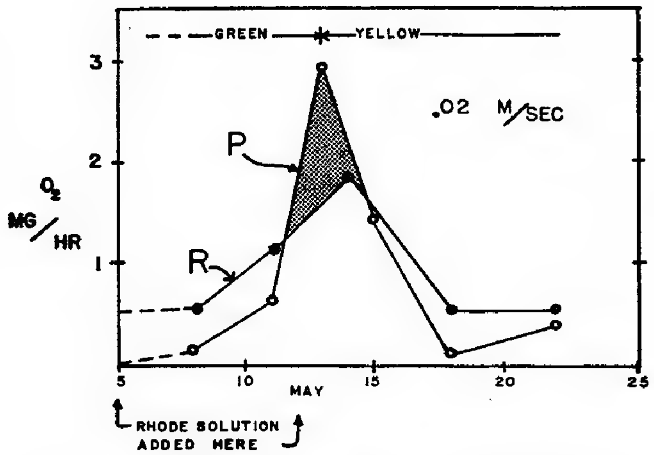

FIG. 6. Community succession and steady state adjustment to low current velocity.

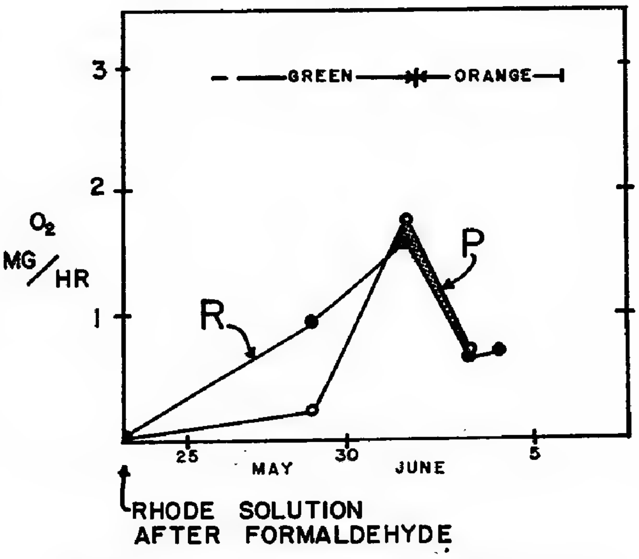

FIG. 7. Community succession and metabolism at high current velocity after sterilization.

F. COMMUNITY SUCCESSION AND METABOLISM AT HIGH CURRENT VELOCITY AFTER STERILIZATION

(FIGURE 7)

While efforts were being made to determine how respiration could exceed photosynthesis for long periods without organic matter, a test was made to determine if there was some inherent oxygen loss somewhere such as in a cavitation action of the pump.

10% formaldehyde was circulated in the system for an hour and then flushed out with a continual flow of tap water for a day. Then the dilute nutrient plankton medium was introduced again with a pinch of aufwuchs saved from the former community. The growth sequence which developed (Figure 7) was similar in community composition, characteristics, and color with a green surface bloom followed by an orange color as the blue greens experienced a pigment change. The initial metabolism measurements following the formaldehyde treatment showed no oxygen increase or decrease thus indicating that there were no non-biological oxygen changes due to the circulation process. During the treatment, visible slime clumps had been removed that had previously been residual through the previous experiments. Thus the total bacterial concentrations and organic storage were diminished at the start of this particular sequence. The metabolism of bacterial slimes in the dark tubing increased more rapidly than that of the algae as shown on the measurements of May 29. The respiration rates were somewhat lower than in earlier experiments at similar high current velocity.

G. EFFECT OF GLUCOSE ON METABOLISM AND SUCCESSION

(FIGURE 8)

On June 5 after another community stoppage was removed, a growth sequence was repeated which followed the usual previous pattern with a green bloom turning toward a yellow steady state as the metabolism diminished. As indicated in Figure 8, 1 gm of glucose was added at the time of the initial algal aufwuchs bloom. Neither photosynthesis nor respiration was stimulated by this supplemental carbohydrate source. Instead the pattern of previous experiments prevailed, with a lowering of metabolic rates and yellowing of the community.

On the other hand when a supplemental inorganic nutrient source was added there was an immediate increase of photosynthesis and respiration. Unlike the stimulatory action shown in an addition of nutrients without organic matter present on April 29, the respiration this time exceeded the photosynthesis in a respiratory bloom.

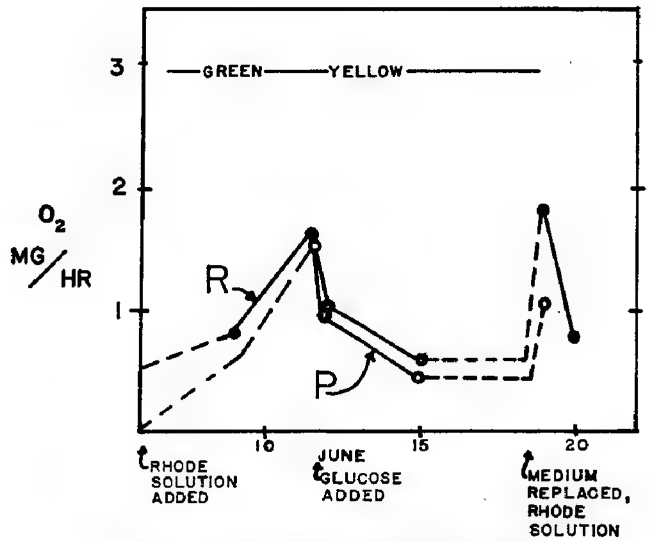

FIG. 8. Effect of glucose on succession and metabolism.

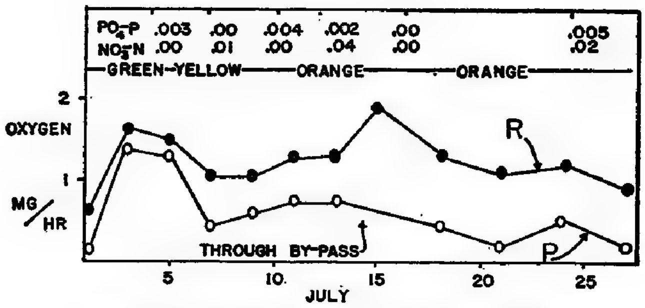

FIG. 9. Characteristics of a steady state based on organic reserves. (Inorganic nutrients self maintained at very low levels).

H. CHARACTERISTICS OF A STEADY STATE BASED ON ORGANIC RESERVES: P/R RATIO LESS THAN ONE

(FIGURE 9)

After cleaning and flushing the visible contents as usual, a new sequence was started with two innovations made on July 1. First, the plastic liner was introduced that permitted indefinite maintenance of the community without slippage and stoppage. Second, all water replacements were made with glass distilled water. The initial establishment of the community over the condenser surfaces followed the previous patterns with a green mat turning yellow after the initial burst of photosynthesis and respiration.

Unlike the two previous sequences the July patterns showed a great excess of respiration over photosynthesis with R values higher than those in the most recent sequences. The maintenance of this excess of R over P in steady state without addition of anything but distilled water indicated a steady organic nutrient supplement. Since the tubes had been flushed out, it was inferred that the residual slime communities in the dark tubes (tygon and plastic covered with aluminum) were holding and storing organic matter for energy sources from previous sequences when these materials were in excess. The glucose in the experiment that had preceded this sequence had apparently been carried over. Another possibility is that dark respiration exceeds light respiration.

On July 15 the circulation was routed through the condenser by-pass for an hour. This by-pass had been exposed to the concentrated solutions of the winter experiments and was known to have developed extensive bacterial slimes which were visibly pink and which had shown strong radio phosphorus uptake. After the water had been routed through the by-pass and returned to the main system, a temporary stimulation of respiratory rate was immediately measured.

From July 10 to August 14 the trend of the respiration rate curve was down. This pattern also suggested a diminishing organic matter source.

I. A STEADY STATE REGIME WITH A BALANCE OF P AND R

(FIGURE 10)

To test the hypothesis that the source of excess respiratory activity was in the dark tubes and that organic matter was stored either on the slimes or in the plastic, the tygon tubing was replaced with glass on August 13. Immediately, the excess respiration disappeared, and after the initial pulse, the photosynthesis became equal to or in excess of the respiratory rate.

On August 18 a mixed organic extract of some former community aufwuchs stored in the refrigerator was added to the system with a small stimulating effect. On September 3 after 10 days without disturbance, a balance of P and R was again in effect. To determine the effect of inorganic nutrients on the respiratory part of the community, inorganic medium was added and the community kept in darkness. After 3 hours, the respiration had increased tremendously but by the next day it was low again. At this time and while the community was still in darkness, glucose was added with an immediate stimulation of respiration which again had returned to normal by the next day.

J. STUDY OF THE VARIATION OF METABOLIC RATE WITH EXPERIMENTAL CHANGES OF CIRCULATION RATE

(FIGURE 12)

As illustrated in Figure 12, a number of series of measurements of photosynthesis and respiration were made of the microcosm under different current velocities and various circumstances over the several months of experiments (Figures 2–11). The communities studied had been growing at one velocity and had been adapted to this

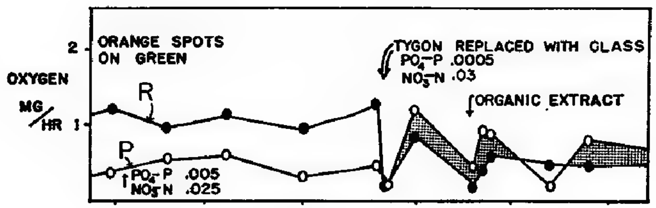

FIG. 10. Change from a steady state with excess of respiration to a balance of photosynthesis and respiration.

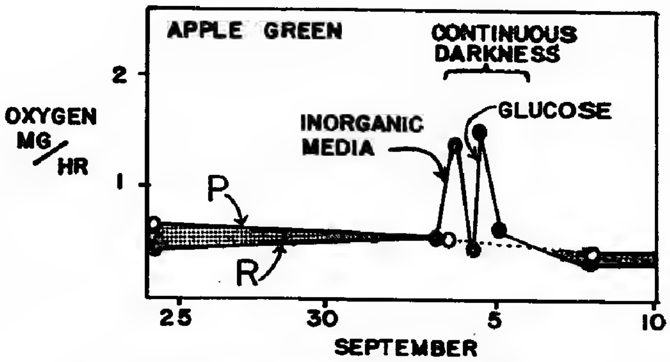

FIG. 11. Inorganic and organic stimulation of respiration under steady state conditions of balanced photosynthesis (P) and respiration (R).

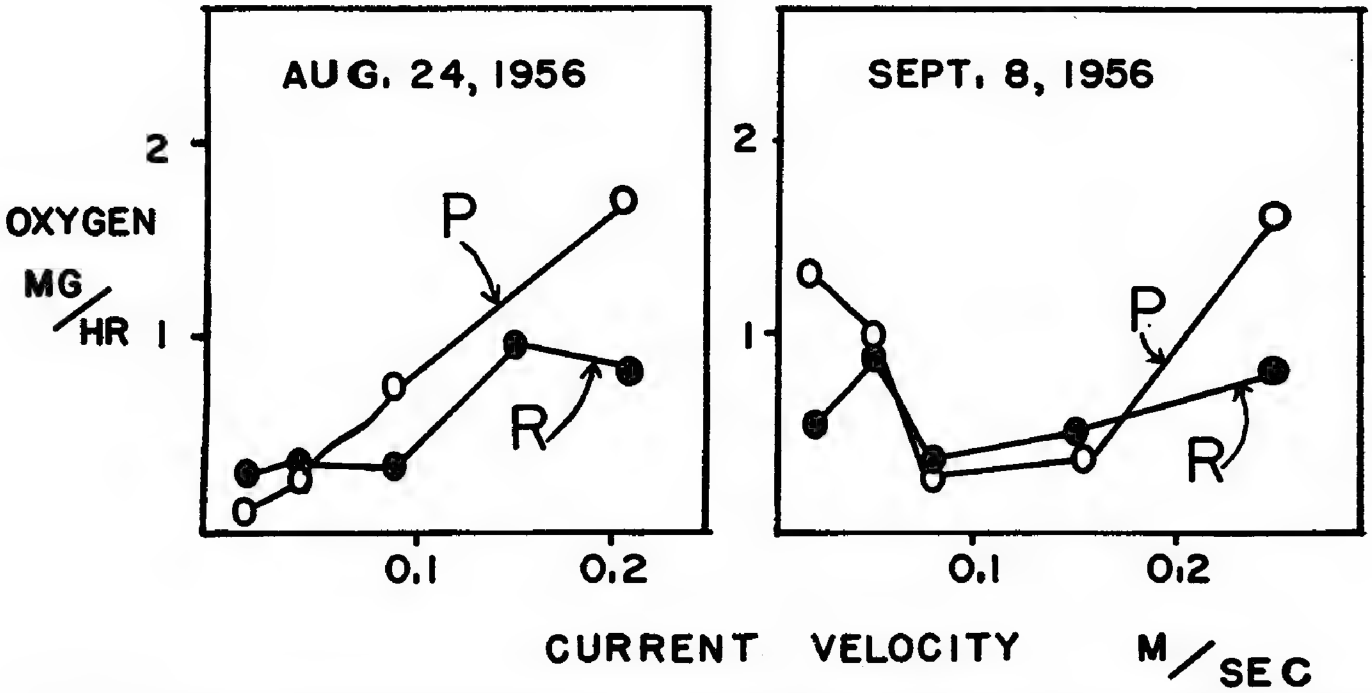

FIG. 12. Two examples of the effect of current velocity on the metabolism of a flowing microcosm in steady state.

velocity. It was found that any change in current velocity caused pronounced effects on the photosynthesis and respiration rates (Figure 12). In several series there was a clear correlation of current velocity with metabolic rate (Figure 12a). In other series there was a maximum or a minimum in the functional relationship of metabolic rate and current velocity (Figure 12b).

If more than one phase of the flow route of raw materials and energy from euphotic zone to regenerating zone and back is current sensitive, it is reasonable that the total metabolism should be a complex function of current velocity. Therefore it is not surprising that the ratio of P/R is modified by the rate of current circulation. Judging in a general way from the current experiments, the total community metabolism possible is greater in high current velocities since the metabolisms of individual plant and animals adapted to high current are greater.

Discussion

METABOLIC ZONATION IN THE MICROCOSM

The distribution of metabolism in the stream microcosm in 3 parts is similar in pattern to that in many streams, lakes, and marine situations. There is (1) a euphotic zone where photosynthesis is occurring, (2) a regeneration zone in the dark where respiratory processes predominate with a release of nutrients, and (3) a circulating medium. The slimes and porous plastics are like the oozes as reservoirs for organic and inorganic storage. As in classical ideas of the balanced aquarium, photosynthesis is dependent on the respiration and vice versa in metabolic symbiosis although separated into separate zones. The discussion by Steele (1956) of a shelf environment, the Fladen ground, or the lake with epilimnion and hypolimnion (Ohle, 1956) may be cited as two examples of macrosystems of similar structure where metabolic rates have been estimated.

THE COMPETITION BETWEEN P AND R FOR INORGANIC NUTRIENTS

When P is equal to R in steady state, the system fulfills the conditions for a closed self regulating cycle system described by Lotka (1925). As Redfield brought out in 1934 such coupling of regeneration and production will tend by a natural selection process to adjust the ratios of the chemical elements in the regenerating system to resemble those in the primary production part of the system.

The photosynthetic and respiratory systems are not, however, necessarily sequentially symbiotic but may exhibit competition also. Where organic matter is available in the community from imports or earlier storage, there may be an excess of respiration over photosynthesis. Under these conditions the bacterial heterotrophs as well as the autotrophs may be limited by the same inorganic nutrients. A competition results. The rapid uptake of radio-phosphorus (Experiment A) in both the condenser euphotic zone and in the regeneration zones of the microcosm is an indication of such competition for phosphorus.

Renn (1937) with experiments on stored sea water showed that the bacterial assimilation of inorganic phosphate was markedly increased if 10 to 60 mg./1 glucose were added. In spite of his own experimental demonstration that marine bacteria with an organic substrate could lower phosphate concentrations below detectable limits, Renn somehow concluded that bacteria do not complete with algal phytoplankton for nutrients. His discussion emphasized the role of bacteria in releasing phosphorus after short life span of a few days. He did not discuss steady state regimes or those where respiration was greater than photosynthesis.

THE EXTRACTION, STORAGE, AND METABOLISM OF ORGANIC MATTER BY AUFWUCHS-SLIME COMMUNITIES

In several of the experimental sequences, there were indications that organic matter could be extracted from the water and stored rapidly during periods of excess dissolved organic matter for use many days later. In experiments C, D, and H there were long periods of time when respiratory metabolism of the whole microcosm exceeded the photosynthetic metabolism (Figures 4, 5 and 9). The quantity of such stored organic matter metabolized during each sequence was determined from a balance sheet calculation using the following equation:

$$P + I = R + S$$

where P is the production, S is the storage, R is the respiration and I the organic matter saved from an earlier time as an import.

Table 1

Balance Sheet Calculations for Experimental Sequences

Community	P/R	Calculation[a]	Total During Sequence Gm	Chlorophyll Per Area Gm/m²	Assimilation Number mg/mg/hr
Fertilized Hyponex, autotrophic March 14, 1956	1.3	P: 2.25 mg/hr for 20 days	1.07	0.38	1.37
		R: 1.50 mg/hr for 23 days	0.83		
		S: final dry weight	1.30		
		I: by difference	1.05		
Dilute media, nutrient rich substrates, heterotrophic April 7, 1956	0.68	P: 1.00 mg/hr for 18 days	0.43	0.12	1.8
		R: 1.25 mg/hr for 21 days	0.63		
		S: final dry weight	0.45		
		I: by difference	0.65		
Dilute media, heterotrophic May 5, 1956	0.74	P: 1.0 mg/hr for 25 days	0.60	0.21	1.0
		R: 1.20 mg/hr for 28 days	0.81		
		S: final dry weight	1.08		
		I: by difference	1.29		
Dilute medium low current heterotrophic June 5, 1956	0.69	P: 0.75 mg/hr for 9 days	0.16	0.095	1.43
		R: 0.75 mg/hr for 13 days	0.23		
		S: final dry weight	0.23		
		I: by difference	0.30		
Dilute medium low current May 24, 1956	0.84	P: 0.65 mg/hr for 17 days	0.27	0.033	3.0
		R: 0.82 mg/hr for 17 days	0.33		
		S: final dry weight	0.20		
		I: by difference	0.26		

[a] P, gross production; R, community respiration; S, storage; I, organic matter (stored previously and metabolized as an import).

In Table 1 are given balance sheet calculations for 5 cases for which data are available. For these calculations the approximations were used that one gram of dry weight of aufwuchs was equivalent to one gram of oxygen metabolism and that the photosynthetic quotient was unity. P and R were obtained from the metabolic graphs. The period of time used for calculating R was greater than for calculating P since the first few days of each sequence were without appreciable plant communities. The storage S was determined as the dry weight of the community aufwuchs removed from the system at the end of the sequence. I was calculated by difference. In most of the cases the magnitude of organic matter metabolized as an energy supplement was apparently as great as the production, even though the growth of plants in the euphotic zone was the visibly conspicuous process.

CHLOROPHYLL AND ASSIMILATION NUMBER

Especially since the studies of Willstatter and Stoll chlorophyll has been related to photosynthetic rates in physiological studies of individual plants. Even closer relationships have been found between chlorophyll of natural communities and their production as in the papers of Manning and Juday (1941), Ichimura (1956), and Edmondsen (1955). Gessner (1949) found similar quantities of chlorophyll per area in lakes, fields and forests. It is of interest, therefore, to determine the relationship of chlorophyll in the microcosm to metabolism and area of the community. A useful function is the assimilation number (ratio of mg carbon-dioxide consumed per hour to mg chlorophyll).

In Table 1 are given the chlorophyll values and assimilation numbers. The quantities of chlorophyll per area are between 0.09 and 0.38 gm/m². These values are lower by a factor of ten than those in terrestrial communities but similar in order of magnitude to those in many aquatic communities. The assimilation numbers between 1.0 and 1.9 mg/hr are similar to those in Silver Springs (0.72) (Odum, 1957) and the Eniwetok coral reef (Odum and Odum, 1955). They are vastly smaller than values of 20 found in algal cultures during successional states (Ryther, 1956).

These comparisons do indicate similarities between the flowing microcosm and the macrocosm. Chlorophyll is apparently as valid a measure of the photosynthesis in steady state adjustment in microcosm as in some similar natural ecosystems.

THE SPECIES DIVERSITY STRUCTURE OF THE COMMUNITIES

Following the procedure used by Yount (1956) on aufwuchs in Silver Springs, counts were made of the species in the aufwuchs of the microcosms at a number of stages during the year. The remarkable tendency for natural communities to have a logarithmic distribution of rarity was utilized to obtain an estimate of diversity. Without actually identifying most species, the cumulative appearance of new species was plotted as a function of the logarithm of the number of individuals examined. These counts were made on bits of aufwuchs placed on microscope slides. The plotted points are given in Figure 13. The lines are fairly straight. The slope of the line is the index of diversity expressed as species/cycle. A cycle is defined as a 10 fold increase in individuals examined. The tendency for straight lines indicates that logarithmic patterns are found in the microcosm as in the Silver Springs System. That the species structure

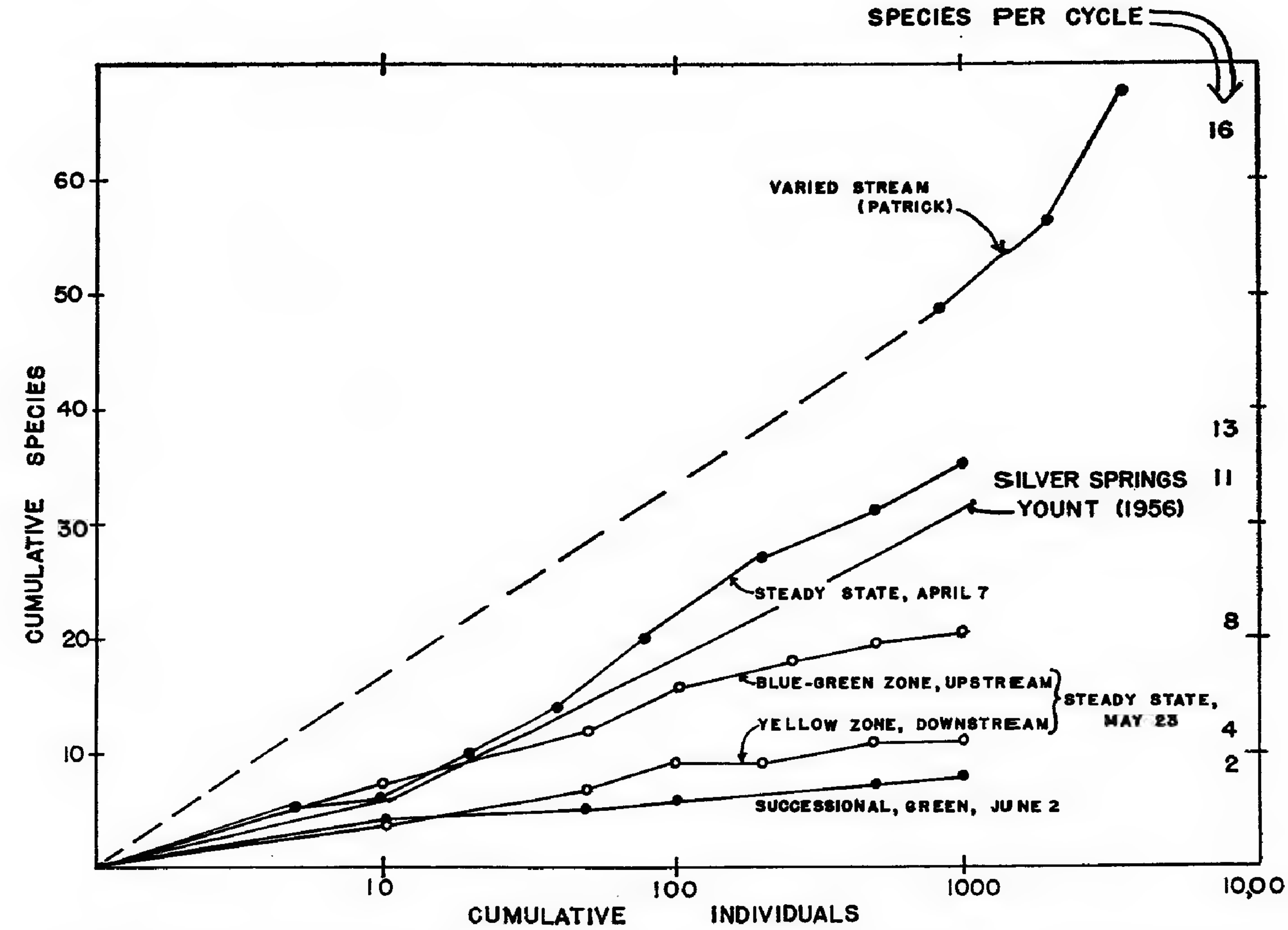

Fig. 13. Cumulative species as a function of logarithm of the number of individuals counted. The slope expressed as species/cycle is the index of diversity used to compare microcosm with macrocosm.

is similar in this respect to typical aufwuchs in nature is a justification for regarding the microcosms as real miniatures.

The species diversities resembled those in Silver Springs regarding relationship to succession. The species variety was less during successional bloom than at steady state.

Dr. Francis Drouet kindly identified the dominant algae of the microcosm as *Phormidium tenue* (Menegh.) Gom. Also present in lesser numbers was *Phormidium inundatum* Kütz, *Plectonema nostocorum* Born, *Anabaena oscillaroides* Bory, *Anabaena variabilis* Kütz, *Stigeoclonium tenus* (Ag.) Kütz, *Scenedesmus quadricauda* (Turp.) Bréb., *Scenedesmus bijuga* (Turp.) Lagerh., *Scenedesmus obliquus* (Turp.) Kütz, and *Calothrix parietina* (Nag.) Thur.

THE YELLOW PIGMENT CHANGE AND ANIMAL SUCCESSION FOLLOWING INITIAL SUCCESSIONAL BLOOM

Kingsbury (1956) found in a culture of a blue-green alga *Plectonema nostocorum* Bornet ex Gomont that with the disappearance of nutrients the aging and cessation of growth of the culture was accompanied by a change in overall pigment in the algae from green to yellow. He was able to restore the original color and stimulate further growth with added nitrate. Kingsbury determined that the yellow pigments were carotenoids. He believed that photosynthesis had stopped or been much reduced in such cells.

As described in the many sequences (Figures 2–11) a similar color change took place in the sessile blue-green algae dominating the microcosm although photosynthesis did not cease entirely. The absorption spectrum of the orange community is in Figure 14. The pattern resembles that given by Kingsbury (1956) with evidence of carotenoid

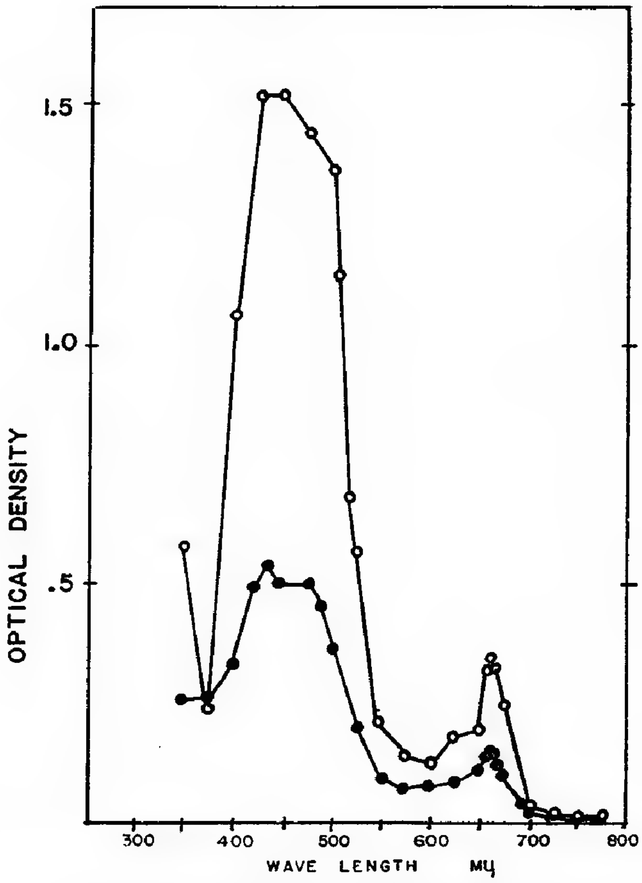

Fig. 14. Absorption spectra of acetone extracts of aliquots of the steady state community. Carotenoids and chlorophyll are present. (1/10 aliquots extracted with 10 cc.)

dominance although chlorophyll is still present.

Throughout the studies the upstream end of the community for about two inches was green while the rest of the community was brilliant orange. In August the condenser tube with community was disconnected and reversed. Within a week the green color had reformed in the upstream end of the community indicating a gradient with respect to the flow of the water. Presumably the green represented the zone where nutrients regenerated in the dark tubes were being removed. Although different in color, microscopical examination did not show differences in species composition or species variety.

Although the meaning of the color shift is not fully understood, it served as a most sensitive visible indicator of the existence of net plant production. Kingsbury postulated that chlorophyll was being used for its nitrogen content and that the plants were metabolically inactive.

In the long steady state series beginning on August 14, the orange color formed as usual but in time disappeared being replaced by a dull green. No nutrients had been added and no spurt in metabolism measured. Examination showed that a large population of herbivores and carnivores had developed in the aufwuchs just as in Silver Springs aufwuchs after the first month. *Arcella* and a flatworm were dominant. In the previous sequences, yellow cells followed the first two weeks algal bloom and did not have appreciable microzoa. It is conceivable that the later development of the animals in the older steady states serves in total function as a means of regenerating nutrients from filamentous algal cells thus preventing the nutrient condition that produces the yellow color.

EFFICIENCY

A rough measurement of incident light energy was made with the help of Dr. J. S. Kirby-Smith of Oak Ridge Laboratories. The galvanometer deflection produced by a standard lamp on an Epply Pyrheliometer was compared at the same distance with the deflection produced by one of the floodlamps. Then a Weston photronic cell was placed opposite the floodlamp so that the microammeter deflection of the photronic cell was found corresponding to a measured quantity of total energy received (1.82 watt/cm^2/microampere). Then the photronic cell was covered with a slit the width of the condenser community and was placed at the microcosm. From the microampere readings, the incident total energy was estimated for the entire condenser of 60 cm length. Rabinowitch (1951:839) figures that 8% of the total energy of incandescent lights of this size is of a wave length suitable for photosynthesis. Using this figure, it is found that the aufwuchs of the microcosm is receiving 0.27 KCal/hr useable light energy. This is of the order of magnitude of full daylight. The maximum gross production of 2.5 mg/hr oxygen figured at 3.5 Cal/gm is 8.7 x 10^{-3} KCal/hr. The production thus is about 3 percent of usable light energy reaching plant level. It is interesting that the efficiencies in the microcosm resemble those of naturally adapted communities in nature (1–8% of visible light energy absorbed).

SUMMARY

1. A flowing water laboratory stream microcosm was constructed in which it was possible to culture and study the growth, succession, and metabolism of whole aufwuchs-slime communities.

2. The communities developing in the microcosm during succession, resembled communities in nature with respect to P/R ratio (0.6–1.3), chlorophyll (0.03–0.38 gm/m^2), assimilation number (1–3 mg/mg/hr), species diversity index (2–13 species/cycle), efficiency (3%), and the low concentrations of nitrate (0.05 ppm) and phosphate (0.005 ppm) maintained in the medium.

3. Under conditions of constant illumination steady state adjustments of whole aufwuchs communities are possible for considerable times with an excess of respiration over photosynthesis as well as with a balance of photosynthesis and respiration.

4. During community succession metabolism was maximal during succession rather than at climax.

5. The metabolism of successional and steady states of whole communities is a complex function of the current velocity. There is a greater metabolism at greater velocities in many cases but not all.

6. Aufwuchs communities show strong powers of taking up both dissolved inorganic and organic nutrients for future use both as raw materials and as an energy source.

7. Pigment changes of the blue-green algal mats of the aufwuchs from green to orange were a sensitive visible indicator of the metabolic condition of the community.

LITERATURE CITED

Ambuhl, H. 1955. Die praktische Anwendung der elektrocheischen Sauerstoff bestimmung in Wasser. Zeit. Fur Hydrol., 17: 123–155.

Brunel, J., G. W. Prescott, and L. H. Tiffany. 1950. The Culturing of Algae, A Symposium.

Bond, R. M. 1933. A contribution to the study of natural food cycles in aquatic environments. Bull., Bingham Oceanographic Coll., 4: 1–89.

Butcher, R. W. 1940. Studies on the ecology of rivers. IV. Observations on the growth and distribution of the sessile algae in the river Hull, Yorkshire. J. Ecol., 28: 210–223.

————. 1945. Studies on the ecology of rivers. VI. The algal growth in certain highly calcareous streams. J. Ecol., 33: 268–283.

————. 1947. Studies in the ecology of rivers. VII. The algae of organically enriched waters. J. Ecol., 35: 186–191.

————. 1949. Problems of distribution of sessile algae in running water. Proc. Int. Assoc. Theoret. and Appl. Limnol. 10: 98–103.

Edmondson, W. T. 1955. Factors affecting productivity in fertilized salt water. Papers in Marine Biology and Oceanography. Supplement to Deep Sea Research, 3: 451–464.

Fox, H. M., B. G. Simmonds and R. Washbourn. 1935. Metabolic rates of Ephemerid nymphs from swiftly flowing and from still waters. Jour. Exp. Biol., 12: 179–184.

Gessner, F. 1937. Untersuchungen uber Assimilation und Atmung submerser Wasserpflanzen. Jb. wiss. Bot., 85: 267–328.

————. 1949. Der Chlorophyllgehalt in See und seine photsynthetische Valenz als geophysikalisches problem. Schweizer. Zeit. f. Hydrologie., 11: 378–410.

————. 1955. Hydrobotanik. I. Energiehaushalt Deutscher Verlag der Wissenschaften, Berlin, pp. 1–517.

Ichimura, Shun-ei. 1956. On the standing crop and productive structure of phytoplankton community in some lakes of central Japan. Botanical Magazine, Tokyo, 69: 7–16.

Kingsbury, John M. 1956. On pigment changes and growth in the blue-green alga *Plectonema nostocorum* Bornet ex Gomont Biol. Bull., 110: 310–319.

Lotka, A. J. 1925. Elements of Physical Biology. Williams and Wilkins, Baltimore.

Lynn, W. R. and D. A. Okun. 1955. Experience with solid platinum electrodes in the determination of dissolved oxygen. I. North Carolina studies. Sewage and Industrial Wastes, 27: 4–9.

Manning, W. M. and R. E. Juday. 1941. The chlorophyll content and productivity of some lakes in Northeastern Wisconsin. Trans. Wisc. Acad. of Sciences Arts and Letters, 33: 363–393.

Odum, H. T. 1956a. Primary production in flowing waters. Limnology and Oceanography, 1: 102—117.

————. 1957. Trophic structure and productivity of Silver Springs, Florida. Ecol. Monographs, 27: 55–112.

Odum, H. T. and E. P. Odum. 1955. Trophic structure and productivity of a windward reef at Eniwetok. Ecol. Monographs, 25: 291–320.

Ohle, W. 1953. Die chemische und die electrochemische bestimmung des molekular gelosten Sauerstoffes der Binnengewasser. Mitteil. Int. Assoc. Theoret. and Appl. Limnol., 3: 1–44.

————. 1956. Bioactivity, production and energy utilization of lakes. Limnology and Oceanography, 1: 139–149.

Redfield, A. C. 1934. On the proportions of organic derivatives in sea water and their relation to the composition of plankton. James Johnstone memorial edition, University Press of Liverpool. 176–192.

Renn, C. E. 1937. Bacteria and the phosphorus cycle in the sea. Biol. Bull., 190–195.

Robinson, R. J. and T. G. Thompson. 1948. The determination of phosphates in sea water. Jour Mar. Res., 7: 33–39.

Ryther, J. H. 1956. Primary production and its measurement. Limnology and Oceanography, 1: 72–84.

Sargent, M. C. and T. S. Austin. 1949. Organic productivity of an atoll. Amer. Geophys. Union Trans., 30: 245–249.

Steele, John H. 1956. Plant production on the Fladen Ground. Jour. Marine Biol. Assoc. U. K., 35: 1–34.

Yount, J. L. 1956. Factors that control species numbers in Silver Springs, Florida. Limnology and Oceanography, 1: 286–295.

Zwicker, B. M. G. and R. J. Robinson. 1944. The photometric determination of nitrate in sea water with a strychnidine reagent. Jour. Mar. Res., 5: 214–232.

Zobell, C. E. and D. Q. Anderson. 1936. Observations on the multiplication of bacteria in different volumes of stored sea water. Biol. Bull., 71: 324.

An Ecological Survey of Baffin and Alazan Bays, Texas

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Introduction

In the summer of 1950, the Texas Game and Fish Commission began an extensive long-term ecological study of the Laguna Madre of Texas, a 130-mile-long hypersaline bay on the South Texas coast. One of the three areas of study was the Baffin-Alazan Bay area (Figures 1 and 2). Field work in this area was started in June of 1951 and was continued until May of 1953. This paper is a portion of a final report to the Texas Game and Fish Commission on this study.

DESCRIPTION OF AREA

At first glance, the Laguna Madre area, which extends from Corpus Christi Bay to the Mexican border and from Padre Island to the mainland, does not, by any means, seem to be the ideal habitat for bay fishes. The major part of the area is in the semi-arid zone where the rate of evaporation is greater than the average annual rainfall. Salinities can vary from nearly 0 to 100 parts per thousand; water temperatures from 0 to 38° C. Much of the area is composed of shallow flats which are uncovered at low tide. Other areas have floors of soft black mud and are void of vegetation. Due to the general shallow condition of the bay, sudden temperature drops take a very heavy toll of fishes. The water is often turbid and at times becomes a dark brown.

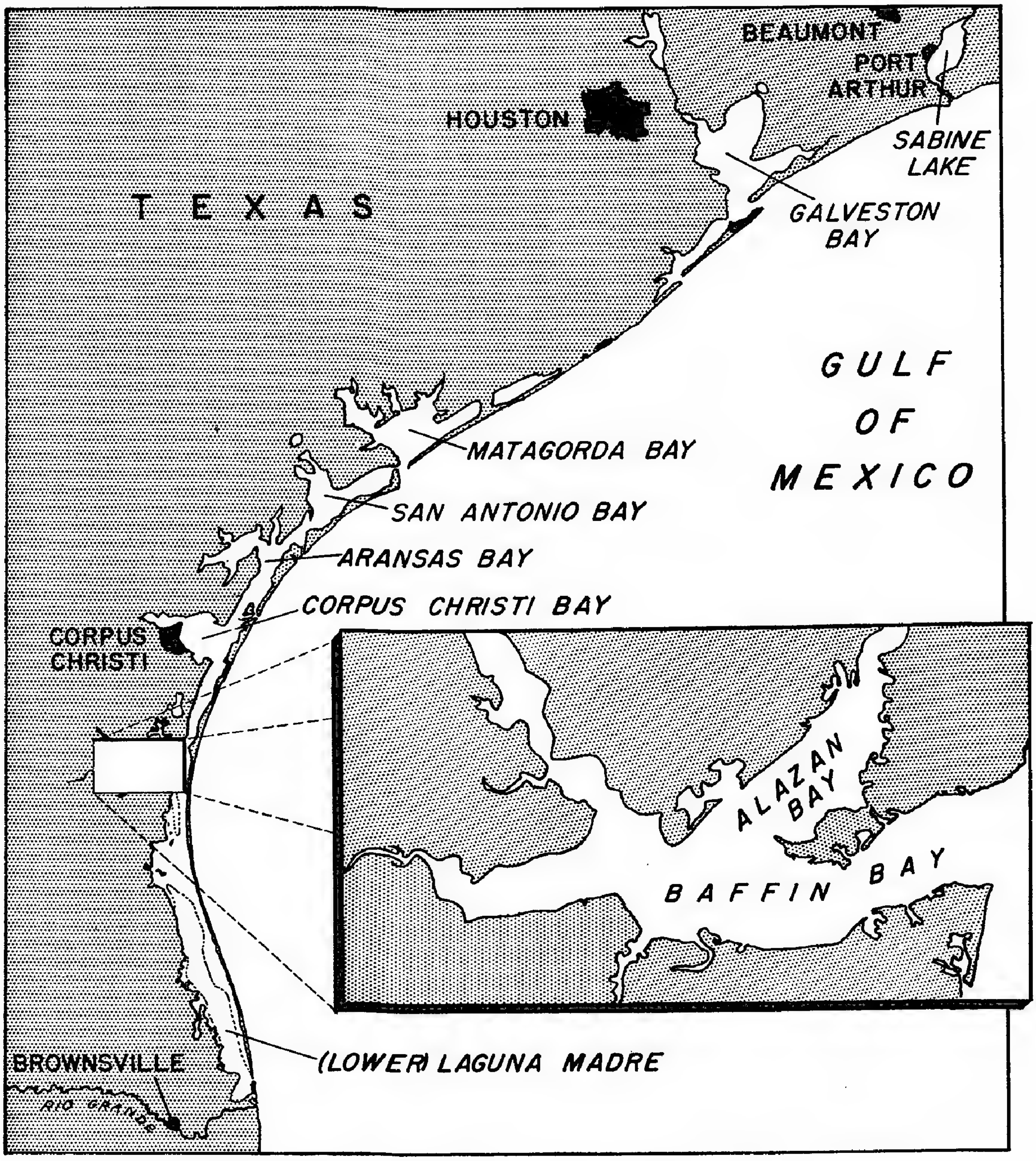
BEAUMONT
PORT ARTHUR
HOUSTON
SABINE LAKE
TEXAS
GALVESTON BAY
GULF OF MEXICO
MATAGORDA BAY
SAN ANTONIO BAY
ARANSAS BAY
CORPUS CHRISTI BAY
CORPUS CHRISTI
ALAZAN BAY
BAFFIN BAY
BROWNSVILLE
RIO GRANDE
(LOWER) LAGUNA MADRE

FIG. 1. Location of Baffin Bay area on the Texas coast.

Baffin Bay, the central and largest bay of the group, is a narrow body of water whose long axis is east and west. The demarcation line of Kleberg-Kenedy Counties runs laterally through the center of Baffin Bay. The mouth of Baffin Bay, which opens into the Laguna Madre, is bordered on the north by Point of Rocks and on the south by Penescal Reef. Baffin Bay is about 18 miles long, 5 miles wide, and 33,560 acres in area at mean high tide. The average depth is 8 feet, and the deepest water in the entire Laguna Madre area is found in this bay between Niggerhead Reef and the entrance to the Laguna Madre, where the water is from 10 to 12 feet in depth. The writer has heard unconfirmed reports of depths of 15 or more feet in the vicinity of Niggerhead Reef.

Alazan Bay, which is entirely within Kleberg County and the King Ranch, extends some 15 miles northeasterly to the mouth of Petronila Creek. The arbitrary boundary between Baffin and Alazan Bays is marked by Middle Reef, which effectively blocks

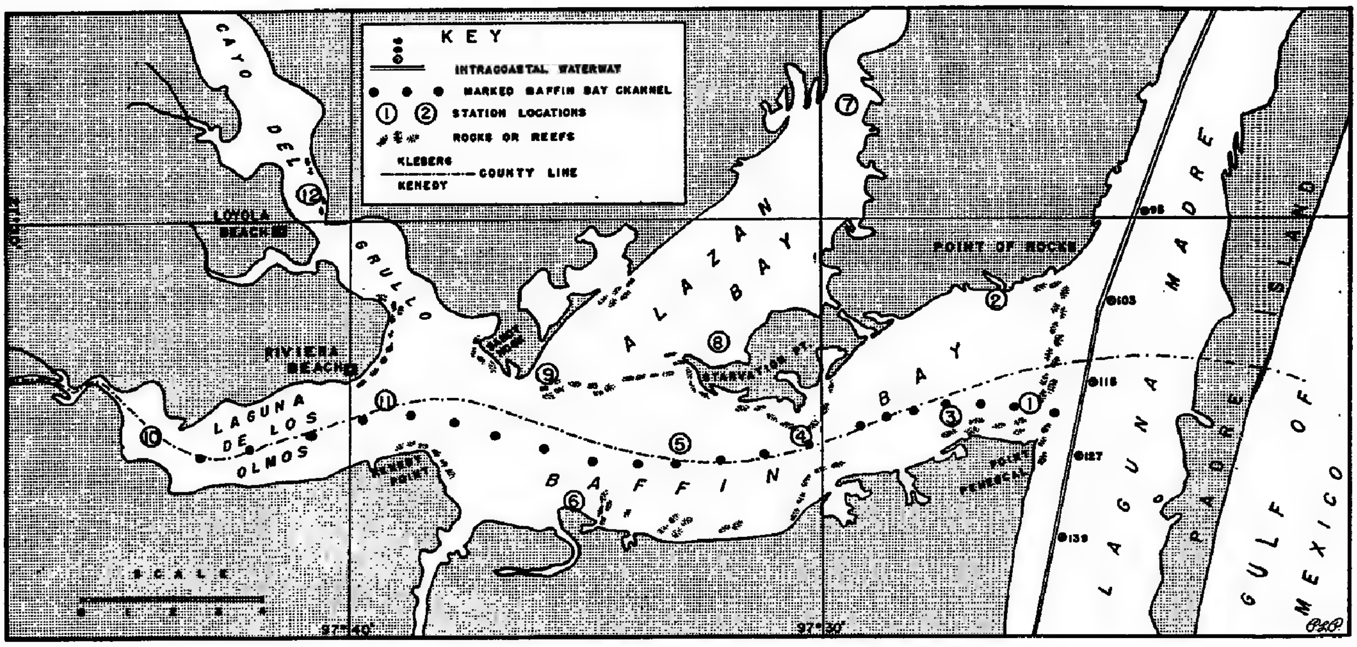
KEY
INTRACOASTAL WATERWAY
MARKED BAFFIN BAY CHANNEL
① ② STATION LOCATIONS
ROCKS OR REEFS
KLEBERG
COUNTY LINE
KENEDY
CAYO DEL GRULLO
LOYOLA BEACH
RIVIERA BEACH
LAGUNA DE LOS OLMOS
KENEDY POINT
SANDY HOOK
ALAZAN BAY
STARVATION PT.
POINT OF ROCKS
POINT PENESCAL
BAFFIN BAY
LAGUNA MADRE
PADRE ISLAND
GULF OF MEXICO
⑦
⑫
②
⑧
⑨
⑪
⑩
①
③
④
⑤
⑥
95
103
115
127
139
SCALE
97°40'
97°30'

Fig. 2. Baffin Bay area.

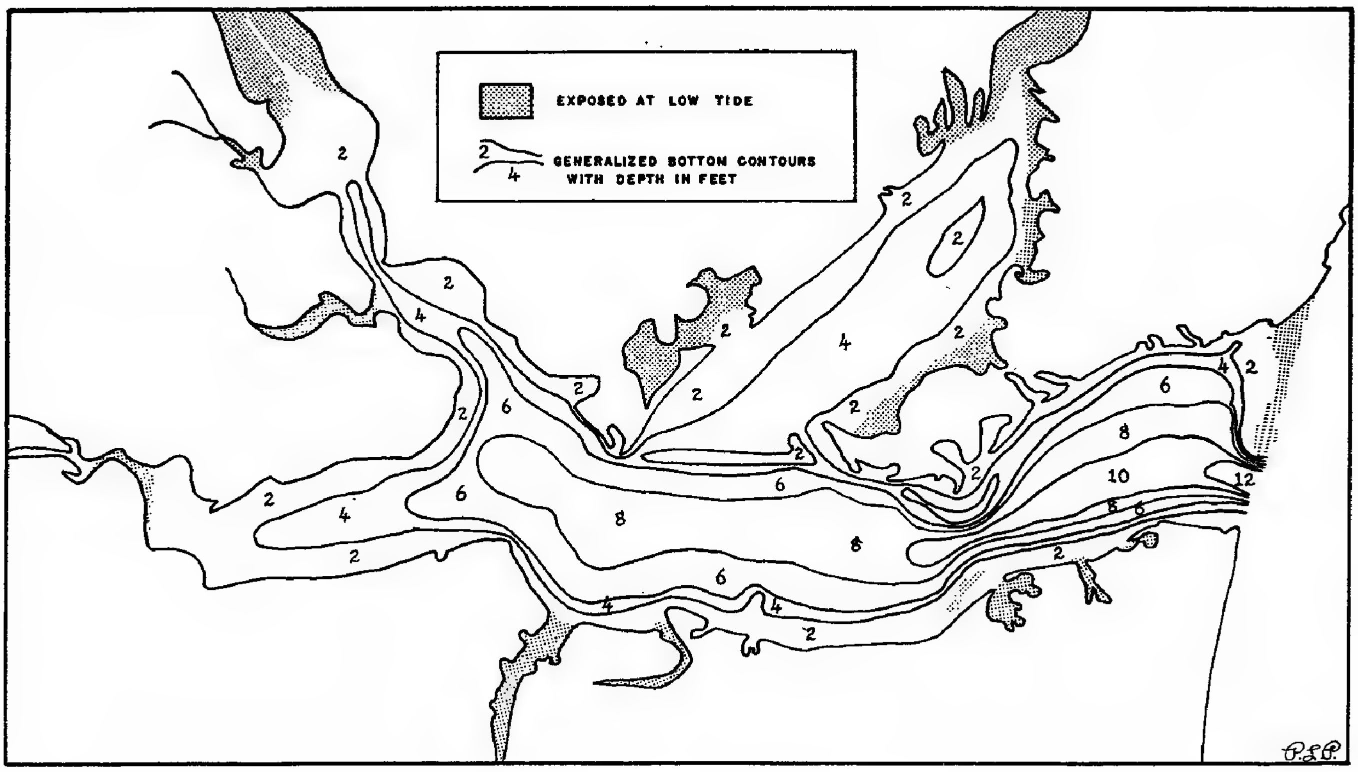
EXPOSED AT LOW TIDE
GENERALIZED BOTTOM CONTOURS WITH DEPTH IN FEET
2
4
6
8
10
12

Fig. 3. Bottom contour of Baffin Bay area.

boat traffic into Alazan Bay. There are three entrances through this reef into Alazan Bay. The most accessible is near Kleberg Point on the west end of the reef. There is another opening between the east end of the reef and the sandbar which extends out from Starvation Point. The other small opening is in the middle of the reef. The last two are not marked and can be used safely only by a few experienced local citizens. At mean high tide, the water area is 14,631 acres and, due to large areas of shallow flats, has an average depth of about three feet.

Cayo del Grullo is in the form of a long arm extending northwestward from the west end of Baffin Bay. The arbitrary line of demarcation from Baffin Bay is a line from Riviera Beach east to Sandy Hook on the King Ranch shore. This bay extends north-

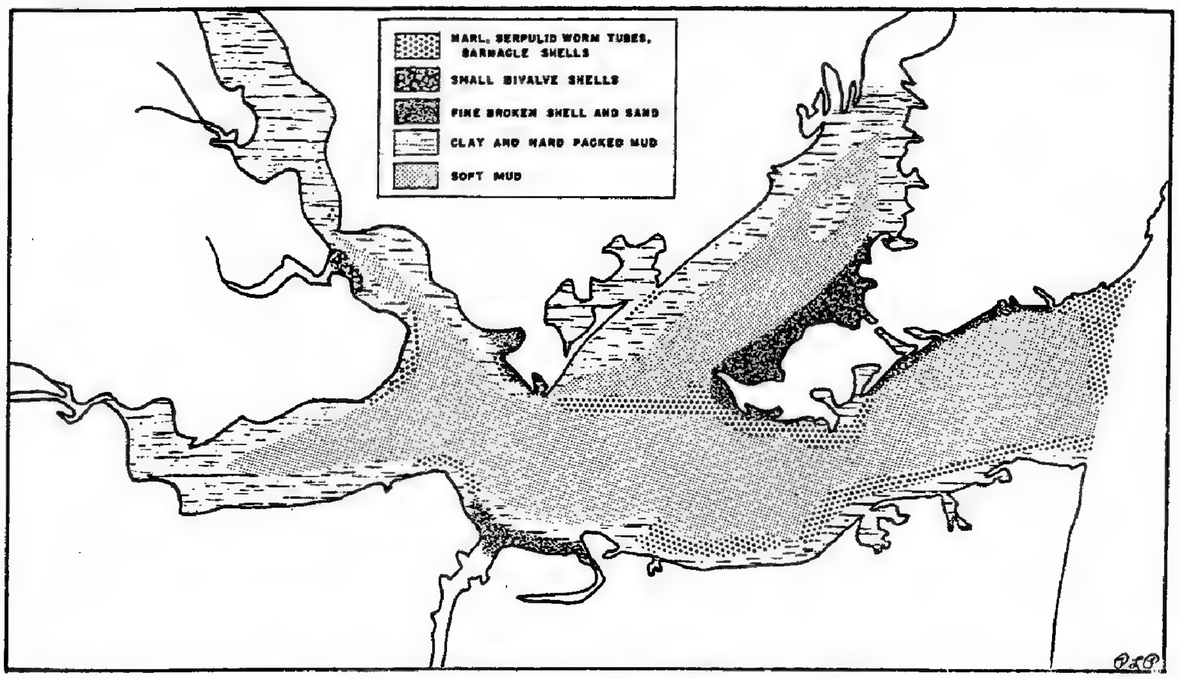
MARL, SERPULID WORM TUBES, BARNACLE SHELLS
SMALL BIVALVE SHELLS
FINE BROKEN SHELL AND SAND
CLAY AND HARD PACKED MUD
SOFT MUD

FIG. 4. Bottom composition of Baffin Bay area.

westward to its arbitrary end at Drum Point, which is six or seven miles from Riviera Beach. Santa Gertrudis, San Fernando, and Escondido Creeks flow into this bay. The average depth is about three feet. The water surface is 7,505 acres at mean high tide.

Salt Creek, or Los Olmos Creek, enters Baffin Bay from the west. It is navigable for about four miles to Field #55 and Williamson's Boat Works and is sometimes called the Laguna de Los Olmos. The average depth is about three feet. The water surface is 3,674 acres at mean high tide.

Cayo Infernillo is a shallow slough extending westward from the west shore of Alazan Bay, whose water surface at mean high tide covers 1,423 acres.

The total water surface for the Baffin Bay system is 60,793 acres at mean high tide. In the deeper waters, the bottom is soft black mud (Figure 4). In the shallow waters along those parts of the shoreline composed of clay bluffs, the bottom is composed of clay eroded from the bluffs by wave action. The bottoms of the shallow water along the more gradually rising shoreline are composed of finely ground shell which has a superficial resemblance to sand. There is very little true sand in the Baffin-Alazan Bay area.

STATIONS

It was the original intention of the biologists assigned to work the Laguna Madre area to locate sample stations according to attached vegetative types. However, since no attached vegetation was found in the Baffin-Alazan Bay area, stations were located according to type of bottom, distance from shore, nearness to reefs, and depths of water. Stations were established to cover, as completely as possible, the entire area. The locations of stations are shown on Figure 2 and were selected as most representative of the environmental factors to be studied.

HISTORY OF THE AREA

After a careful inspection of the Baffin Bay area shoreline, it became apparent that many locations had been used as camp sites by Indians in years past. Indian arrow points were found at Kleberg and Starvation Points. Bits of flint and pottery were common at bluffs several miles north of Drum Point. The most significant discovery was that of a camp ground on the east shore of Cayo del Grullo opposite Loyola Beach. At this site, a large pile of oyster shell and thousands of black drum (*Pogonias cromis*) otoliths were found, along with arrow points and other signs of Indian habitation.

The Karankawa tribe lived along the shore from the Oso Creek of Corpus Christi Bay northward. Dr. Price[1] states that all the evidence from hundreds of oyster bearing middens that he mapped in the 1920's and those mapped by Mr. George C. Martin on Copano Bay shows "that Karankawa Indians carried oysters and other shellfish in hide sacks from the beds directly to the first elevated land to camp and ate them. They did not, so far as the records show, carry them in boats from a reef to some distant point." Dr. Price also states that the Karawankas "did go about from point to point in the water, but the distribution of oysters that we have mapped does not show any evidence that they wandered around when they had a food load."

Dr. Price stated in the same communication that "Mr. C. F. H. von Blucher who died in the 1930's and was a county surveyor for many decades said that his father, also a surveyor and a careful scientist, said that the Indians used to carry oysters from Nueces Bay in hide sacks moving to the first high ground. The two Bluchers' observations covered the period from 1846 to 1880 when the last Karankawas disappeared."

Dr. Price supports the author's theory that these oysters found on the midden grew in Cayo del Grullo, unless the Indians occupying the midden were not of the Karankawa tribe, in which case their habits might have been different.

If we assume that oysters once grew in the Baffin Bay area, the area must have enjoyed a much lower salinity, since oysters could not tolerate the present high salinity. Since water circulation in the Laguna Madre proper would have little effect on Cayo del Grullo and other tertiary bays of the area, the surrounding watershed must have experienced a sufficiently high annual rainfall to keep the maximum yearly salinity at or below 45 parts per thousand.

The bottom of Cayo del Grullo is now covered with three to eight feet of very soft mud, which could not support the weight of an oyster; therefore, the extinction of the oyster population in the area may be due either to the heavy siltation resulting from heavy runoff in past years or the reduction of annual rainfall of recent years which resulted in the increase in salinity, whichever came first.

If salinities and turbidity were once low enough to support an oyster population, it is possible that the floral and faunal populations included marine grasses and a more diversified faunal community. Dr. Price further stated that Mr. H. N. Fisk of the Humble Oil and Refining Company found a layer of marine plant remains buried in the 10 to 12 foot bed of clay that blocks the Laguna Madre south of Baffin Bay and that five per cent of the seeds were viable. Dr. Price stated that "conditions for the plants would have been good if the former inlet at the Santa Cruz ranch site on Padre Island had been open. This inlet was open long enough to develop a good tidal delta and it has not been appreciably modified since."

Dr. Price also stated that "there are evidences that the washover channels opposite the mouth of Baffin Bay (occasionally active) may have been permanent inlets at one time. If so, it is likely that a larger flow from the streams would have been necessary to maintain them, as the bay is poorly shaped and oriented to support a tidal exchange in large enough quantity without the addition of a good stream discharge." Dr. Price estimated the time that Fisks plants were growing to be approximately half-way between 1800 and 1830 (when Fisk thought the Laguna Madre was open) and 1950. The picture painted by this discussion is a far cry from the Baffin Bay and adjacent Laguna Madre of today.

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[1] Dr. W. Armstrong Price, Consulting Geologist and Oceanographer, Corpus Christi, Texas. Personal communication—January 24, 1957.

The effect of reduced runoff on the Baffin Bay watershed in recent years has contributed greatly, among other things, to the ecological changes in the Laguna Madre proper. Reduced circulation in the Laguna Madre was caused by reduced runoff, formation of serpulid reefs, shoaling of the Flour Bluff and Point of Rocks areas, and complete filling in of 24 miles of the Laguna Madre in Kenedy County, possibly by the hurricane of 1919, although this latter development is generally believed to have been a bit more gradual (Collier & Hedgpeth, 1950). Circulation between the Laguna Madre and Baffin Bay has been affected by serpulid reefs (not growing now, as far as the author could ascertain) which effectively block water exchange for three-fourths of the Baffin Bay mouth.

Other undesirable conditions which have helped to change the ecology of the area are the failure of Yarborough Pass, the continued drought, and the completion of a fill causeway from Flour Bluff to Padre Island.

SALINITY AND TIDES

Attempts were made to visit each of the twelve stations at least once every month. The physical and meteorological data gathered on each trip included the general weather conditions; wind direction and velocity; air, water surface, and water subsurface temperatures; salinity; pH; and turbidity of the water. Low, mean, and high salinities, pH, and turbidities are given in Table 1 for the twenty visits to each station during a period of nineteen months, from September of 1951 to March of 1953.

Salinities were determined by a modification of the Knudsen chlorinity determination

TABLE 1

Physical Data from September, 1951 to March, 1953

	Salinity (parts per thousands)			pH			Turbidity (per cent transmission)[c]		
Station	Low	Mean[a]	High	Low	Mean[a]	High	Low	Mean[a]	High
1	36.30	53.00	63.00	7.30	7.88	8.28	72.5	89.5	98.0
2	24.85	52.75	62.00	7.35	7.95	8.20	83.0	92.5	100.0
3	33.60	53.65	61.80	7.35	7.90	8.20	71.0	89.0	97.5
4	31.50	53.40	64.75	7.55	7.98	8.65	64.0	82.3	97.5
5	27.30	51.35	65.40	7.45	7.85	8.20	70.5	89.3	95.5
6	20.00	50.90	62.40	7.30	7.90	8.48	71.5	84.0	99.0
7	1.40	50.70	75.05	7.40	7.90	8.25	5.0	72.5	95.0
8	18.60	50.10	69.95	7.50	7.80	8.25	56.0	82.0	97.5
9	14.60	50.35	67.30	7.45	7.95	8.20	56.5	85.5	97.0
10	11.25	49.60	73.70	7.50	8.05	8.55	53.0	85.5	99.0
11	15.50	49.93	69.90	7.40	7.85	8.35	64.0	85.5	98.0
12	7.65	54.40	69.00	7.55	7.95	8.40	52.0	87.5	97.0
	Low	Ave. Mean[b]	High	Low	Ave. Mean[b]	High	Low	Ave. Mean[b]	High
	1.40	51.68	75.05	7.30	7.91	8.65	5.0	85.4	100.0

[a] Means were compiled by averaging the data from 19 analyses.

[b] Average means are the result of averaging the means from all 12 stations.

[c] Cylindrical tube, 18 mm. diameter inside. Optical density = 2 log (per cent transmission).

method. A 0.1594 normal solution of silver nitrate was used to titrate 10 ml. of sea water, to which 1 ml. of a five per cent solution of potassium chromate had been added, and the volume of silver nitrate was read as salinity in parts per thousand. A Beckman model M pH meter was used in pH determination, and a Lumetron Photoelectric Colorimeter model 400 G was utilized for turbidity.

The water level fluctuations of this bay area are affected primarily by precipitation, wind, and the long period solar semi-annual tides. The long-range water level is controlled by precipitation and long period tides. The forces of precipitation and the semi-annual tides usually work together, as rainfall on the surrounding watershed is most likely to occur during the spring or fall flood tides. The heavy rains which fell in September of 1951 raised the water level more than four feet at Loyola Beach. Although this level was constantly declining, the rise in water level, in conjunction with the fall tides, kept the bay level abnormally high through the spring of 1952.

The short range water level is controlled by the winds. This cause and effect was observed by the author on numerous occasions. For example, the immediate effect of a strong north wind is to blow the water out of Alazan Bay and Cayo del Grullo and pile it up on the Kenedy shore of Baffin Bay. The ultimate effect of this wind would be to pull the water out of Baffin Bay into the Laguna Madre, as the water in the Laguna is pushed south. The immediate effect of the prevailing southeasterly or southerly winds would be to blow the water from Baffin Bay and pile it up in Alazan Bay and Cayo del Grullo. The ultimate effect would be to pull the water out of Baffin Bay as the water in the Laguna is pushed north. A west wind would push water out of Baffin Bay, and an east wind would push water into Baffin Bay, but there are seldom winds from these directions. During periods of little or no wind, the water level would tend to equalize, and at these times the effects of tides are slightly more noticeable.

The only tides whose effects can be noticed above the normal effects of the wind are the tides in the spring and fall. These high tides may change the normal winter and summer water levels as much as 12 to 18 inches, and because this rise brings in water from the usually less saline upper Laguna Madre, the salinity of Baffin Bay tends to become lower. This slight freshening effect can bring about an influx of fish, particularly in the fall. This situation will be discussed more thoroughly under the heading of "Biological Components," along with the effects of other physical and meteorological phenomena on the various marine populations.

Before the completion of the Intracoastal Canal in 1946, which joined both bodies of the Laguna Madre, salinities soared as high as 102 parts per thousand near the mouth of Baffin Bay (Collier & Hedgpeth, 1950). Many fish were killed by this hypersaline condition.

Prior to this dredging of the Intracoastal Canal, the Game and Fish Commission attempted to alleviate the high salinities of the area by cutting a pass through Padre Island at Murdock's Landing, some five miles southeast of the mouth of Baffin Bay. The objective was to develop an exchange of water between the hypersaline Laguna Madre and the less saline Gulf of Mexico.

Yarborough Pass was first completed in April of 1941 and remained open for five months. The second dredging was completed in November of 1942, when the pass remained open for five more months. In May 1944, the pass was reopened but closed shortly thereafter. The fourth attempt to keep the pass open was completed in November of 1944, and the pass closed the next month. During the four years of dredging, the pass remained open for a period of 10 months, and a reasonable flow was maintained for only six months.

Salinity determinations made by Gunter during the dredging period showed that salinities in the Laguna Madre were affected only within one half-mile of the pass, and that the Laguna Madre salinity was altered only one-half of one per cent (Gunter. 1945b). Gunter has discussed in detail the reasons for the failure to keep Yarborough Pass open and why the pass, while open, had little effect on reduction of salinities or of water exchange.

The Intracoastal Canal accomplished what Yarborough Pass could not, that is, it provided a more effective water exchange and a resulting salinity reduction for the Laguna Madre. With the prevailing southeast wind to set up a northerly current, the waters of the Gulf enter the system through Brazos Santiago Pass at Port Isabel and at times flow the entire length of the Laguna Madre, emptying into Corpus Christi Bay. This seasonal but timely exchange has benefited the flora and fauna of the Laguna Madre to a great extent, not only by lowering the excessive summer salinities, but by providing ways of escape for fish to waters of lower salinity or temperature in times of need. Because of the still inadequate exchange of water in Upper Laguna Madre and lack of rainfall in the area during the past few years, the salinity has occasionally become high enough to cause fish to leave the area. This was noted by the author during the summer months of 1951 and 1952. Although salinities still rise as high as 80 parts per thousand, no major fish kills due to hypersalinity have been noted in the Laguna Madre since the completion of the canal.

The fish pass through Padre Island in the north Laguna Madre area, produced even less benefit in Baffin-Alazan Bays than in the Laguna Madre as far as the reducing of the water salinity is concerned.

Due to pressure brought to bear on the Game and Fish Commission by the general public, to bring about still lower maximum salinities in the upper Laguna Madre, Yarborough Pass was reopened on February 14, 1952 and remained open for about three weeks. Data obtained on February 19, five days after the opening indicated that the pass did little to help Baffin Bay. (Salinities in the Baffin Bay area ranged from 32 parts per thousand to 46 parts per thousand.) The brief opening of the pass lowered the salinity at Station 1, which is located at the mouth of Baffin Bay just a few hundred yards from the Intracoastal Canal, only 3.85 parts per thousand. The salinity at Station 2 dropped an insignificant 0.2 parts per thousand. All the remaining 10 stations experienced an increase in salinity ranging from one part per thousand to almost three parts per thousand. It appears obvious that cutting Yarborough Pass can not help Baffin Bay by lowering salinity, since there is no circulation through the Baffin-Alazan Bay area. There may have been some water circulation in the upper Laguna Madre, although this is doubtful.

On the other hand, heavy rains in the Kingsville, Falfurrias, Alice, and Robstown areas between the dates of September 11 and September 15, 1951, lowered the salinity of most of Baffin Bay 20 to 60 parts per thousand and kept the salinity of the entire area below 60 parts per thousand throughout the following summer. Although the Intracoastal Canal will probably keep Baffin Bay salinities below 85 parts per thousand, runoff from the Kenedy, Kleberg, Jim Wells, and Nueces County watersheds is the only effective means of lowering salinities further in the Baffin-Alazan Bay areas. The torrential rains of September, 1951, brought thousands of tons of marketable fish into Baffin and Alazan Bays, and because the headwaters of the bays were fresher than the Laguna Madre, the fish remained there for at least seven months. The heavy rains which flooded Alice, Kingsville, and Robstown during August, 1953 also brought millions of gallons of water to the bays, and fish moved into the area again.

Biological Components

Plankton samples were obtained by towing a Number 12 (125 mesh) plankton net on a one meter ring just beneath the surface of the water for a period of three minutes. Samples were taken at each station every month. Although the volume of water which passed through the net varied with actual speed of the boat, direction and velocity of wind and current, etc., maximum effort was made to keep techniques constant so that all samples taken in the area could be compared to some degree. No attempt was made to study bacteria, foraminifera, and nannoplankton.

Amphipods were collected by hand from submerged rope and barnacle-encrusted posts. Molluscs were collected by the use of a dredge of one-fourth inch mesh hardware cloth towed behind a boat. Shrimp, crabs, and bottom fishes were taken by the use of a 10 foot shrimp (otter) trawl. Smaller specimens were collected by placing a one-fourth inch mesh liner or a cheesecloth liner inside the trawl. A one-fourth inch mesh seine was used along the shores, occasionally lined with cheesecloth, to capture shrimp, crabs, and juvenile fish.

Fish were also collected by rod and reel, trot lines, and by the use of three-, four-, and five-inch stretched mesh gill nets. Creel catches by sports fishermen and the landings by commercial fishermen were also used for production data.

As a result of two years of collecting by these methods, the following annotated check list of biological components was compiled for the Baffin Bay area.

VEGETATION

CHLOROPHYCEAE (Algae)

Enteromorpha clathrata (Roth) was found in very limited quantity on the piers and pilings at Loyola Beach in the summer of 1952.

Cladophora sp. One insignificant scrap of this algae was taken from a sunken skiff at Loyola Beach in the summer of 1952.

BACILLARIOPHYCEAE (Diatoms)

Coscinodiscus sp. Not too common. Taken in limited number near the mouth of Baffin Bay at all times.

Navicula sp. Fairly common. Found at periods of salinities below 35 parts per thousand in Cayo del Grullo and Laguna de Los Olmos.

Amphiprora paludosa (William Smith) was found at all times and at all stations. Most plentiful of diatoms. Quite common but not in large numbers.

INVERTEBRATA

PROTOZOA

Ceratium hirundinella (Müller) Bergh. Only dinflagellate in the area. Fairly common at all times at all stations.

Vorticella sp. One colony noted on the scrap of *Cladophora* algae taken during the summer of 1952 at Loyola Beach.

COELENTERATA

Phortis sp. Common throughout the area in the spring months. A nuisance in collecting plankton samples.

CTENOPHORA

Beroë ovata Chamisso and Eysenhardt. Occurred with *Phortis* and common at the same time.

MOLLUSCA

Mulinia lateralis Say. Once common throughout the area but now confined chiefly to the head of Alazan Bay (Station 7) although some of the once barren areas of Baffin Bay are now being repopulated. Important as food for the black drum.

Anomalocardia cuniemeris Conrad. Once common in Cayo del Grullo and Laguna de Los Olmos but now reduced to a very few scattered specimens. Of equal importance as food for drum with *M. lateralis*.

ARTHROPODA

COPEPODA

Acartia tonsa (Dana). Very common throughout the area at all times and in all stages of development. Comprises almost all of one of the heaviest plankton populations on the Texas coast. 250,000 individuals were found on the average in the three-minute plankton tows which were taken in a standard manner. Values ranged from 6,000 to one million individuals per tow.

Metis jousseaumei (Richard). Not common. Found at mouth of Baffin Bay in spring and early summer in varying numbers.

Caligus rapax Milne Edwards. Parasitic. Found in large number infesting the entire black drum population in winter months of 1951–52. Drum not affected by the parasitism.

CIRRIPEDIA

Balanus amphitrite Darwin. Not common. Few specimens found near the mouth of Baffin Bay.

Balanus eburneus Gould. Found throughout the area wherever places of attachment occurred. Population limited due to shortage of places of attachment.

AMPHIPODA

Gammarus mucronatus (Say). Found in large numbers clinging to the webbing of a gill net set in Cayo del Grullo in the summer in 1952.

DECAPODA

Penaeus setiferus (Linnaeus). Not common. A few specimens found along the shorelines of Cayo del Grullo and Laguna de Los Olmos during the winter months.

Penaeus aztecus (Ives). Very common throughout the area during the late spring and early summer for a period of about six weeks. Otherwise, not found.

Callinectes sapidus Rathbun. Fairly common, but not in quantity. A few specimens found in the more shallow waters during the summer months.

Of the 21 recorded species of flora and invertebrate fauna, 10 species are either rare or are found only at the junction of Baffin Bay and the Laguna Madre and are present only for short periods under certain conditions. This leaves 11 species which can be considered normal residents of the area:

DIATOMS
  Navicula sp.
  Amphiprora paludosa
DINOFLAGELLATES
  Ceratium hirundinella
COELENTERATA
  Phortis sp.
CTENOPHORA
  Beroë ovata
MOLLUSCA
  Mulinia lateralis
COPEPODA
  Acartia tonsa
CIRRIPIDIA
  Balanus eburneus
AMPHIPODA
  Gammarus mucronatus
DECAPODA
  Penaeus aztecus
  Callinectes sapidus

VERTEBRATA

ELASMOBRANCHII

Dasyatidae

Dasyatis sp. Not common. Several sting rays were taken in gill nets at Station 12 following the heavy rains of September, 1951. A few more were noted on the sand flats on the east shore of Alazan Bay, and one sting ray was taken at Station 10 in March of 1952.

TELEOSTOMI

Lepisosteidae

Lepisosteus spatula (Lacépède). Not common. Thirty-four alligator gar were taken by gill net at Station 12 in the four months following the rains of September, 1951. These gar may have come down the creeks into the bay with the overflow from the several man-made lakes on the King Ranch.

Ariidae

Bagre marinus (Mitchill). Usually rare. The gafftopsail catfish was noted in the vicinity of Station 1 in the early summer months but not in quantity.

Galeichthys felis (Linnaeus). The common hardhead or sea catfish is very plentiful at all times throughout the area, as would be expected, although it is most common during the summer months. Male hardheads, captured by gill net in June and July of 1952, were noted to be carrying eggs.

Megalopidae

Tarpon atlanticus (Valenciennes). Rare. One specimen was noted jumping off Riviera Beach on February 10, 1952 in the vicinity of Station 11.

Elopidae

Elops saurus Linnaeus. A few skip-jacks were taken by gill net at Station 12 throughout the year but never in quantity. This fish is more common, at times, near the junction of Baffin Bay and the Laguna Madre.

Clupeidae

Dorosoma cepedianum (Le Sueur). Normally, not common. This fish, the gizzard shad, was quite abundant in Cayo del Grullo in the two months following the heavy run-off in September of 1951. Like the alligator gar, we believe this fish came from the lakes on the King Ranch.

Brevoortia sp. Not common. A few large menhaden appeared at Station 12 in the late fall of 1951. Some small specimens (one to two inches) were taken in trawl samples in the Laguna de Los Olmos in the summer months.

Synodontidae

Synodus foetens (Linnaeus). Rare. One lizard fish was taken at Niggerhead Reef (Station 4) in October of 1952.

Cyprinodontidae

Fundulus similis (Baird & Girard). Not common. A few sepcimens of the gulf killifish were found in the Laguna de Los Olmos during the warmer months.

Cyprinodon variegatus variegatus Lacepede. Very common. The broad killifish, locally known as the "chubby" is very common in the more shallow water (less than three inches) throughout the entire area and in the tide pools in all but the coldest months.

Atherinidae

Menidia beryllina peninsulae (Goode & Bean). Very common. The tidewater silverside is quite abundant in this region, particularly in the waters from two to four feet deep in the Laguna de Los Olmos and Cayo del Grullo.

Mugilidae

Mugil cephalus Linnaeus. The common or striped mullet is the most numerous fish in the area. It is found at all locations throughout the year in astounding numbers, particularly in the more shallow waters and near the serpulid reefs. This fish appears to be able to adjust to almost any range in temperature and salinity. Most specimens range in size from four to 14 inches, although a number of large mullet weighing up to nine pounds were taken in gill nets at Station 12 after the heavy rains in the fall of 1951. These large specimens apparently are not common to the area. No mullet eggs or juveniles of less than three inches were ever taken.

Stromateidae

Peprilus paru (Linnaeus). Rare. One specimen of the harvest fish was taken by gill net at Station 12 on January 4, 1952.

Centropomidae

Centropomis undecimalis (Bloch). Rare. One snook or pike was taken by gill net at Station 12 on New Year's Day, 1952.

Haemulidae

Orthopristis chrysopterus (Linnaeus). Rare. The pigfish or "piggy" was noted in very small numbers, at times, in the vicinity of Point of Rocks and Penescal Reefs adjacent to the Laguna Madre. The waters of Baffin Bay appear to be too saline for this common bay fish.

Sparidae

Lagodon rhomboides (Linnaeus). Fairly common. This fish is fairly common throughout the area except during the coldest months, although not as plentiful as in the grassy flats of the Laguna Madre proper. The pin perch or pinfish is most numerous in the vicinities of rock reefs, marine installations, or near human habitation during the summer months.

Sciaenidae

Cynoscion arenarius Ginsburg. Uncommon. The sand trout is not common to the area, although a few specimens have been taken by rod and reel in the spring and fall months at the junction of Baffin Bay and the Laguna Madre.

Cynoscion nebulosus (Valenciennes). Common. The well-known spotted sea trout is an important sports and commercial fish of the area, although its number varies throughout the year. Trout of seven to eight pounds have been taken recently, but the average is considerably less.

Bairdiella chrysura (Lacépède). Not too common. The silver perch or "yellowtail" was present in small numbers in Cayo del Grullo in the fall of 1951.

Sciaenops ocellatus (Linnaeus). Common. The channel bass or redfish is also an important food and sports fish of the area and can be taken throughout the area. Large schools of nearly mature redfish can be seen along the north shore of Baffin Bay between Starvation Point and Point of Rocks during September and October. Zero class reds can be found during the summer months near the serpulid reefs. One and two year class redfish are commonly taken on trot lines during the spring and fall months.

Leiostomus xanthurus Lacépède. Not common. The spot croaker can be found throughout the area during the warmer months but not in quantity.

Micropogon undulatus (Linnaeus). Fairly common. The golden croaker is present in small quantities along with the spot croaker but is usually of small size (three to five inches). Large schools of mature croakers can be expected at the mouth of Baffin Bay each fall, but the date of their arrival varies from year to year.

Pogonias cromis (Linnaeus). Common. The black drum is the most abundant food fish of the area. Adult drum are plentiful throughout the area at all times but chiefly during the fall and winter months. Drum populations increase as temperatures and salinities drop.

Trigilidae

Prionotus sp. Not common. Several large sea robins were taken in gill nets during the late autumn of 1951 in Cayo del Grullo.

Bothidae

Paralichthys lethostigma Jordan & Gilbert. Fairly common. The southern fluke, our commercial bay flounder, is found in small numbers throughout the area but is usually of small size, the majority being under 12 inches.

Although the number of species of fish recorded during this project seems large considering the excessive salinity, 26 species in 17 families, three species were found only at the junction of Baffin Bay and the Laguna Madre and cannot be considered residents of the Baffin Bay area. Two additional species, the gizzard shad and alligator gar, may have entered the bay when the fresh waters behind the dams on the King Ranch overflowed during the heavy rains of 1951. Six more species, normally found in the Gulf and primary bays, entered during abnormal conditions of low salinity and high water level and remained for only a short time. Five additional species, although present at most times, are present in very few numbers and must be considered rare, or at least not common to the area. This leaves but ten species which can be considered normal residents of the area:

Arridae
    Galeichthys felis
Cyprinodontidae
    Cyprinodon variegatus
Antherinidae
    Menidia beryllina peninsulae
Mugilidae
    Mugil cephalus
Sparidae
    Lagodon rhomboides
Sciaenidae
    Cynoscion nebulosius
    Sciaenops ocellatus
    Micropogon undulatus
    Pogonias cromis
Bothidae
    Paralichthys lethostigma

Discussion

VEGETATION AND INVERTEBRATES

It may appear odd that a bay of some 60,000 acres would not contain some type of spermatophyte vegetation. It would seem that the salinity, turbidity, depth, and type of bottom would be sufficiently varied to support at least one species of attached vegetation at some place in the area. All commercial fishermen contacted who have been well acquainted with the bay since the turn of the century cannot recall having ever seen a growing marine plant. The prevailing southeasterly winds bring viable rhizomes of *Diplanthera wrightii* into Baffin Bay from the Laguna Madre, but these have not taken root. Several attempts were made during the spring of 1952 in the flats between Point of Rocks and Niggerhead Reefs to transplant *Diplanthera wrightii*, *Thalassia testudinum*, and *Ruppia maritima*, but all attempts met with failure.

Apparently, high salinity does not explain the absence of attached vegetation in the Baffin Bay area. The waters of the Laguna Madre in Kenedy and Kleberg Counties experienced the same high salinities during the 1940's and still have a good growth of vegetation. The lack of shoal water could partly explain the absence in Baffin Bay but only in part, since much of Alazan Bay is shoal although void of vegetation.

It appears to the writer that the normally high turbidity of the water, which prevents the penetration of sunlight to the bay floor, even in very shallow areas, may be the deciding factor in explaining the absence of attached vegetation in the Baffin Bay area. Of course, there may be other contributing factors.

High salinity and the lack of suitable places of attachment could explain the shortage of macroscopic algae. None of the Gulf forms could tolerate the hypersalinity, and such forms as *Enteromorpha* and *Cladophora*, which do occur, are kept down by radical changes in salinity.

The high turbidity of the water might explain, at least in part, the scarcity of diatoms, since sunight is necessary for photosynthesis of these plants, as well as the spermatophytes.

Heavy populations of living *Mulinia lateralis* and related species, were once common to the entire area. The majority of the shorelines of Baffin Bay proper, as well as Alazan Bay and Cayo del Grullo is composed largely of the dead shells of these molluscs. Using a grid system and a dredge of one-fourth inch mesh hardware cloth, some 300 samples were taken during the two-year period. In Alazan Bay only one deposit of living *Mulinia lateralis* was located and that at Station 7 at the head of the bay. A few scattered specimens of *Anomalocardia cuniemeris* were found near Riviera Beach.

Although the high salinities of the area in the early 1940's undoubtedly destroyed large portions of the molluscan populations, extensive populations were noted in the Laguna Madre of Kleberg and Kenedy Counties, while few to none were found in Baffin Bay proper. The writer believes that the scant live shell population might have been caused by pollution outbreak at the Celanese Corporation plant at Bishop, Texas, which was blamed for many dead fish and odorous water at one time prior to 1951. Since this effluent (nature unknown to the writer) was reportedly discharged into San Fernando Creek, which empties into Cayo del Grullo and into Baffin Bay proper, this could explain the sparing of the *Mulinia* population at the head of Alazan Bay. The potential pollution problem at the Celanese plant appears to have been solved, since large areas of Baffin Bay proper are now populated with *Mulinia* at this time, and the molluscan populations of the area in general appear to be increasing.

The copepod *Acartia tonsa*, although listed in the literature as a brackish water copepod was found in every plankton sample taken in the area; however, neither Baffin Bay nor any part of it could possibly be called brackish. With salinities ranging from 1.4 parts per thousand to 75 parts per thousand and turbidity from 5 per cent to 100 per cent of light transmission, *Acartia tonsa* appears to flourish in a wide range of conditions. The density of this copepod was the reason that the normal 10-minute plankton tow was reduced to three minutes. In spite of the scarcity of all other planktonic forms in Baffin Bay, the density of *A. tonsa* gives this bay one of the heaviest zooplankton populations on the Texas coast.

Another free living copepod, *Metis jousseaumei,* was found at times near the mouth of Baffin Bay but was believed to be part of a heavier population of this copepod which is known to frequent various portions of both the upper and lower Laguna Madre, principally in Kenedy County.

A parsitic copepod, *Caligus rapax,* infected the entire black drum population during the winter of 1951-52. The number of copepods per drum ranged from one to several hundred, although the fish apparently suffered no ill effects from the parasitism.

Although a few specimens of the white shrimp *Penaeus setiferus* were found during the late winter months along the shorelines of Laguna de Los Olmos and Cayo del Grullo, this species is of little importance to the area. Each year during the late spring and early summer, however, a large population of grooved shrimp, *Penaeus aztecus,* migrated into the bay. When summer temperatures and salinities soared, they left en masse, and not a trace of them was found again until the next year. These grooved shrimp remained in the area for only a month to six weeks, affording large quantities of food for young trout and redfish for a short period in the year. Many trout and immature redfish follow the shrimp into the bay each year and give the sport fishermen of the area some little chance of success for a time. These shrimp are the juvenile forms of the commercial brown shrimp, ranging in length from two to four inches, and are part of the vast juvenile grooved shrimp population which uses the entire Laguna Madre as its nursery ground every spring and summer.

The blue crab, *Callinectes sapidus,* although present in small quantities during the summer months, is of little commercial or biological importance. The few specimens are mostly large males.

MULLET AND BAIT FISHES

Of the three most common bait fishes in the area, the common or striped mullet, *Mugil cephalus,* is the most important. It is found in all sizes from four to fourteen inches in all locations and at all times. Populations are greatest in the more shallow waters and near the serpulid reefs.

The mullet is able to withstand all adverse conditions. Extreme temperature and salinity variations have little or no effect on their numbers. Although many tons of mullet were killed in the hypersaline conditions in 1945 and in the cold spell of 1951, no decrease in their total population was noticed.

Although ripe male and female mullet are common in the area, the mullet does not appear to spawn in the area under study. No mullet eggs or juveniles under three inches were ever taken, although there were repeated attempts to do so.

During the fall of 1951, following the heavy rains on the watershed, many large mullet of nine pounds were taken in the bay. It is believed that these large mullet came from the artificial lakes on the King Ranch.

The fingerling mullet of four to six inches is the most acceptable food for the two and three year class redfish. Larger mullet are used as food by the larger trout. Cut mullet is a popular bait for bottom trot lines and is taken by trout, reds, and drum.

The tidewater silverside, *Menidia beryllina peninsulae,* is particularly common in Laguna de los Olmos and Cayo del Grullo, where it forms the major portion of the diet of the two- to four-year class trout. These fish are believed to spawn in those areas, since the larval forms were taken, although no eggs were found.

The broad killi-fish, *Cyprinodon variegatus,* locally known as the "chubby" is very abundant in the area but lives only in the shallowest waters and tide pools. It is seldom found in waters of more than three inches in depth and therefore is of little importance as food for fish except drum. It is, however, an important part of the diet of the wading shore birds. The chubby is greatly in demand by trot line fishermen as bait, since it does not decay as rapidly as mullet and is readily accepted by redfish and drum. The chubby spawns in these shallow water areas in the early spring, the juvenile forms are common by May and June.

THE SPOTTED SEA TROUT

The spotted sea trout, *Cynoscion nebulosus,* is an important sports and commercial fish of the Baffin Bay area, although its numbers vary throughout the year. It is conspicuous by its absence when salinities reach 55 parts per thousand. There is no evidence to indicate that the trout spawn in this area. Nowhere in Baffin Bay are there suitable trout spawning grounds with comparatively fresh, clear water and shallow grassy flats with sand bottoms. However, young trout of from two to four inches in length have been taken in a minnow seine in the vicinity of Station 10 in the summer. The trout of Baffin Bay range from this small size to the large "sow" trout of seven and eight pounds. The smaller trout were found to feed mainly on the silversides, while the larger trout feed almost entirely on mullet. The relatively poor catches of trout by the various hook and line methods may be attributed to the peculiar feeding habits of the trout. A large trout will invariably find the largest mullet it can handle and proceed to swallow it. The mullet will generally range from one-half to two-thirds the size of the trout. Many trout taken in the gill nets were found to contain mullet so large that the belly of the trout would be greatly distended, and several inches of the mullet's tail would still protrude from the trout's mouth. Experiments made by keeping these trout for several days before killing them for stomach analysis showed that the total digestion of the mullet would take from two to three days. Therefore, if a large trout were to feed only 10 to 15 times per month, the chances of taking this trout on a baited hook would be very slim. Although trout fishing in the Baffin Bay area is, at times, good, the writer believes that it is generally below a par set by the Laguna Madre proper. The majority of trout in Baffin Bay are of the two- to four-year class. These trout feed mostly on silversides, even during the period when shrimp are present. They are found chiefly in the vicinity of the serpulid reefs, and therefore are difficult to capture with trammel nets. Gill nets could be used with some success, but trout captured in this manner are usually in too poor a condition to tag and release. Rod and reel were used at times to sample the trout population of the area, but only eleven trout were tagged during the survey period, none being reported recaptured to date.

THE REDFISH

The redfish, *Sciaenops ocellatus,* is another of the important food and game fish of the Texas coast, and it, too, appears regularly in Baffin Bay. The redfish spawns along the beaches of the barrier islands of Texas but spends most of its life in the bays. The heavy mullet population of the area makes Baffin Bay an ideal feeding ground for the redfish, since fingerling mullet is a favorite food. During the months of September and October, large schools of bull redfish are often seen feeding in the shallow waters along the north shore of Baffin Bay between Stations 2 and 9. Although an occasional fish is taken by fishermen, the school seldom suffers appreciable depletion because of the size of the fish, and the proximity of rock reefs make boat navigation hazardous. Attempts were made to capture fish from these schools for tagging by trammel net, but due to the depth of water (10 feet) in which the fish were traveling and the proximity of the reef, none was captured.

During late spring and early summer, many redfish hatched in the Gulf the previous fall can be taken throughout the area. They are usually too small to interest either sports or commercial fishermen. Periods of high salinity will, however, cause these fish to leave the region for less saline areas.

Only six redfish were tagged in Baffin Bay, and none has been reported recaptured to date. The poor results of redfish capture can be explained by the fact that redfish have a tendency to fight in a gill net until they break free or are dead from exhaustion; therefore, gill nets were not used expressly for the capture of redfish. During the summer months when rat reds, as the zero year class redfish are called, were present, gill nets could not be used because the reds died quickly in the nets due to the high water temperature.

THE BLACK DRUM, TAGGING RECOVERIES

The black drum, *Pogonias cromis*, is by far the most important food fish of the area. Baffin Bay, along with the Laguna Madre proper, represents the center of the black drum population throughout its entire range. The shallow, warm, turbid waters, combined with a muddy bottom, are ideal as a drum habitat. Also, the Laguna Madre and Baffin Bay area contains (or did, until a few years ago) large beds of live shell, which comprise the chief food of the drum. Very young drum will feed on various small marine animals and bits of organic material, but adult drum feed primarily on molluscs, of which *Mulinia lateralis* is most abundant.

Drum of all sizes can be found in the Baffin Bay area. Sciaenid eggs believed to be those of this species were found at Station 2 in late March of 1952. Ripe and spent adults were taken during the same month. Young drum of from two to three inches were found during June and July, 1951, in the Intracoastal Canal at the mouth of Baffin Bay (Marker 127). Young of from five to seven inches, called "butterfly drum," are found in great numbers in Cayo del Grullo and in Salt Creek during the winter months. Adults can be found throughout the area at any time of the year, although the number will decrease in the area as the temperture and salinity increases.

It is true that the Laguna Madre area generally is the most saline bay on the Texas coast. It is also true that more drum are found in the locality than in any other area of the coast. However, they are present here in spite of the high salinity, not because of it. While the black drum can survive in waters of higher salinity than can many of our other food or game fishes, it will invariably move toward the fresher water where it will remain, providing it can find food there. During the late summer and early fall of 1951 when the salinity of Baffin Bay was at its usual high, the area was particularly void of drum. In September, from the 11th to the 15th, precipitation on the surrounding watershed lowered the salinity at the head of Alazan Bay from 55.3 parts per thousand to 1.4 parts per thousand and the Alazan Bay average from 54.7 parts per thousand to 11.5 parts per thousand. The salinity at Loyola Beach dropped from 62.5 parts per thousand to 9.6 parts per thousand. Within one week after the first runoff entered the bays, more drum were congregated at the mouths of the flowing creeks than the writer believed existed in the entire Laguna Madre area. This occurred just eight months after a cold spell killed a conservatively estimated 60 to 90 million pounds of fish, mostly drum, and chiefly in the Laguna Madre area.

Immediately following a rainfall which brings about an appreciable runoff, the freshest water in the area can be found at the mouths of the creeks. The drum congregate in these areas. In periods following prolonged dry spells, these waters become saline due to evaporation and are then the most saline waters in the area. During such periods, Baffin Bay may be practically void of this species.

Of the 993 fish tagged in the Baffin Bay survey, 966 were drum. The proportion of the black drum to the other fish tagged shows approximately the ratio of this fish to the others in the area. Recoveries are recorded in Table 2.

The chief method of drum capture during the winter months was the gill net. Each gill net was 500 feet long, of five inch stretched mesh, 14 meshes deep, and hung on the halves.

TABLE 2

Tag Returns from Baffin Bay (November, 1951 to March, 1957)

Tag No.	Species	Date Tagged	Where Tagged	Date Caught	Where Caught	Disposition and Remarks
A6256	Drum	1-31-52	Station 12	3-14-52	Drum Point	Moved in one mile in 43 days
A3064	Drum	2-28-52	Station 12	3-7-52	Laguna Marker 175	Moved out and south 30 miles in 10 days
A6188	Drum	1-26-52	Station 12	2-10-52	Redfish Bay	Moved out and south at least 50 miles in 15 days
A6224	Drum	1-27-52	Station 12	2-22-52	Rio Hondo	Moved out and south 90 miles in 26 days
3783	Drum	11-4-51	Station 12	2-20-52	Riviera Beach	Moved out 4 miles in 106 days
3775	Drum	11-5-51	Station 12	1-29-52	Station 12	No movement in 84 days
3768	Drum	11-5-51	Station 12	2-19-52	Penescal	Moved out 20 miles in 105 days
A6222	Drum	1-27-52	Station 12	1-28-52	Station 12	Moved out 2 miles in 1 day
A6085	Drum	1-22-52	Station 12	2-6-52	Oso Bay	Moved out, up Laguna, through Corpus Bay into Oso Bay, 63 miles in 15 days
3781	Drum	11-4-51	Station 12	1-14-52	Station 12	Moved out 2 miles in 70 days
A6093	Drum	1-22-52	Station 12	1-26-52	Station 12	Found dead
3772	Drum	11-4-51	Station 12	11-27-51	Station 12	No movement—23 days
3664	Drum	11-4-51	Station 12	12-5-51	Station 12	No movement—24 days
3603	Drum	11-6-51	Station 12	11-9-51	Station 12	No movement—3 days
4729	Drum	10-19-51	Station 12	3-1-53	Pita Island	Moved out and north 50 miles in 16 months—grew one and one-fourth inches
3609	Drum	11-6-51	Station 12	5-31-52	Green Brush Arroyo Colorado	Moved out and south 90 miles in seven months
A3008	Drum	2-14-52	Station 12	3-15-52	Drum Point	Moved in one mile in 30 days
3627	Drum	11-15-51	Station 12	3-30-52	Drum Point	Moved in one mile in 30 days
A3099	Drum	2-29-52	Station 12	3-26-52	Three Sloughs	Moved out and up Alazan Bay 13 miles in 26 days
1835	Drum	2-10-52	Station 12	3-27-52	Three Sloughs	Moved out and up Alazan Bay 13 miles in 46 days
A3042	Drum	2-15-52	Station 12	2-23-52	Station 10	Moved out and up Laguna de Los Olmos 10 miles in 8 days
A6262	Drum	1-31-52	Station 12	2-23-52	Station 10	Moved out and up Laguna de Los Olmos 10 miles in 24 days
3613	Drum	11-6-51	Station 12	1-24-54	Padre Island Causeway	Out and north 60 miles in 799 days
3602	Drum	11-9-51	Station 12	2-14-54	Bulkheads	Out and north 63 miles in 826 days. Grew 70 mm.

Of the 966 drum tagged in Baffin Bay, twenty-four have been recaught and reported. Three of these moved out of Baffin Bay south into Redfish Bay and the lower Laguna Madre. Another traveled out of Baffin Bay, through the Laguna Madre and Corpus Christi Bay, and into Oso Bay. This 63-mile journey was accomplished in 15 days and was undoubtedly encouraged by the spawning instinct, as it occurred at the beginning of the spawning season for drum. This seems to indicate that while many drum spawn in Baffin Bay and the northern Laguna Madre, many others from this area travel to the Oso Bay area, which has long been recognized as a spawning ground for drum.

Another drum traveled the 50-mile route out of Baffin Bay and through the northern Laguna Madre to Pita Island in 16 months (near the causeway connecting Flour Bluff and Padre Island in Nueces County). Measurements indicate that this fish grew 30 mm. (one and one-fourth inches) in that period of time, which seems to be a slow rate of growth. However, this drum measured 25 inches when tagged, and a drum of this size adds length very slowly, adding considerable weight instead. Two others traveled to the Padre Island causeway in 799 and 826 days.

The remaining drum were taken within 30 miles of where they were tagged. Those caught within a short period of time after they were tagged may have been just feeding, since the water was of low salinity, ideal for the presence of drum. Others may have remained in the area to spawn, since many of them were tagged at about the same time that fertilized drum eggs were found in Baffin Bay.

The presence of parasitic copepods infecting the drum, the predominating size of the fishes of the various schools, their predominate coloration and general physical condition, along with records of tag returns leads the writer to believe that the various schools of drum in the area are slowly but constantly moving. Coloration of fishes in several schools will vary to black, bonze, and gray. That the fish of one school may be fat and healthy, whereas those taken the next week are thin and in poor condition, indicates that they are from different schools. One week, the average size of the fish taken will be a pound or more different in weight than the average of those taken the week before. Many drum have been taken in gill nets several times at the same location within a week of their original tagging. One persistent tagged drum was taken daily on nine consecutive days following its original tagging.

The movement of drum in Baffin Bay during these fairly static periods of salinity seems to be caused by a search for food. It appears that a school wanders into Baffin Bay and spends weeks or even months cruising slowly about in search of food and then leaves. This search for food in Baffin Bay may be caused by a shortage of food in the Laguna Madre. It may be habit or instinct that brings drum into an ancestral feeding ground. Unfortunately, the food seems to be no longer there, and it is a mystery to the writer how so many drum can exist on such a small supply of live molluscs.

The main spawning of black drum seems to occur in March, April, and May, although this period is sometimes extended. In addition, a shorter spawning period occurs in the early fall. This split spawning period, plus the extensions of the periods themselves, tend to complicate the study of life cycles, age determination, rate of growth, and time of maturity. It will be some time before sufficient information is gathered to write an accurate life history of the black drum.

Present information shows that the main spawning of the black drum occurs in the early spring in Baffin Bay, as well as in the Laguna Madre and in such previously discovered spawning grounds as Oso and Nueces Bays, and the shallow waters of Corpus

Christi Bay. A larval drum which hatches from the egg in the spring will reach a length of 5 cm. (two inches) in May, 6.2 cm. in June, 14 cm. in August, 20 cm. by November, and 22.5 to 25 cm. (nine to ten inches) at the end of its first year. The drum reaches sexual maturity at the end of one and one-half years (12 inches) and will spawn for the first time at the end of its second year (Miles, Simmons and Breuer, 1952).

Ten flounder were captured by gill net at Station 12. All were of small size and were taken following heavy rains which brought about abnormal bay conditions.

Although trout, redfish, and flounder may be noted in relative abundance in the Baffin Bay area at times, these species are generally less abundant than in the Laguna Madre proper. The water, as a rule, is too saline and turbid to present the ideal habitat for these fish. Even though some enviable catches of trout and redfish have been brought in by both commercial and sports fishermen from the Baffin Bay area, trout and redfish landings are much below a par set by the adjacent Laguna Madre.

Summary

1. The Baffin-Alazan Bay phase of the Game and Fish Commission's general study of the Laguna Madre system of Texas began in June of 1951 and terminated in May of 1953. The area studied consisted of Baffin and Alazan Bays, Cayo del Grullo, Los Olmos Creek, and Cayo Infernillo, the entire area covering about 60,000 acres at mean high tide.
2. Physical characteristics which make the area different from most Texas bays are the soft mud bottom, the absence of tidal effect except for wind tides, the lack of suitable stream discharge, and the resulting lack of water circulation and exchange.
3. The salinity for the two-year period averaged 51.68 parts per thousand, pH 7.91, and the turbidity 85.4 measured by per cent of light transmission.
4. All biological components were studied except bacteria, foraminifera, and nannoplankton. Biological characteristics which are most noteworthy are the complete absence of spermatophytic vegetation, the almost complete lack of microscopic algae, and the extremely heavy copepod population.
5. In general, the total number of both plant and animal species is very limited, but those forms which are present are available in large quantity. Among the factors which limit the number of species are the normally high salinity, the normally turbid condition of the water, and the inaccessibility to the Gulf of Mexico.
6. Of 993 fish tagged in the area, 966 were black drum *(Pogonias cromis)*. Although some drum spawned near the mouth of Baffin Bay, their presence in the area seemed to be correlated with food, particularly during the fall and winter months.
7. Because of its geographical location and its physical and meteorological aspects, this hypersaline area is unlike any other bay area on the Texas coast, resulting in a great faunal difference from other bays under study.

LITERATURE CITED

Burkenroad, M. D. 1951. Some principles of marine fishery biology. Publ. Inst. Mar. Sci. Univ. Texas, 2(1) : 181–212.

Collier, Albert and Hedgpeth, Joel W. 1950. An introduction to the hydrography of tidal waters of Texas. Publ. Inst. Mar. Sci. Univ. Texas, 1(2) : 121–194.

Gunter, G. 1945A. Studies on marine fishes of Texas. Publ. Inst. Mar. Sci. Univ. Texas, 1 (1) : 1–190.

————. 1945B. Some characteristics of ocean waters and the Laguna Madre. Texas Game and Fish. 3(11) : 7, 19, 21—22.

Hedgpeth, Joel W. 1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. Publ. Inst. Mar. Sci. Univ. Texas, 3(1): 109–224.

Miles, D. W., Simmons, E. G., and Breuer, J. P. 1952. The spotted sea trout, redfish, and drum of the Texas gulf coast. Marine Lab., Texas Game and Fish Comm. (Unpublished Manuscript).

Miles, D. W. 1952. The life histories of the spotted sea trout, *Cynoscion nebulosus,* and the redfish, *Sciaenops ocellatus.* Marine Lab., Texas Game and Fish Comm. (Unpublished Manuscript).

Pearse, A. S. 1952. Parasitic crustacea from the Texas coast. Publ. Inst. Mar. Sci. Univ. Texas, 2(2): 7–42.

Pearson, John C. 1929. Natural history and conservation of the redfish and other commercial Sciaenids on the Texas coast. Bull. U. S. Bur. Fish., 44 (1928): 129–214.

Pulley, T. E. 1952. An illustrated check list of the marine mollusks of Texas. Texas Jour. Sci., 4(2): 167–199.

Simmons, E. G. 1952. The Cedar Bayou fish trap. Final report. Marine Lab., Texas Game and Fish Comm. (Unpublished Manuscript).

————. 1957. An ecological survey of the upper Laguna Madre. Publ. Inst. Mar. Sci. Univ. Texas, 4(2).

U. S. Department of Interior, Fish and Wildlife Service 1954. Gulf of Mexico, its origin, waters and marine life. U. S. Gov't Printing Office, Washington, D. C.

An Ecological Survey of the Upper Laguna Madre of Texas

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Introduction

Considerable interest has been shown in the Laguna Madre because of its unusual salinity conditions. This report is concerned with the plant life, invertebrates and vertebrates of the area and the relationship of these to basic physical and biological factors in the environment.

Gratitude is expressed to Dr. Thomas E. Bowman and Dr. F. A. Chace, Jr. of the United States National Museum who identified amphipods, shrimp and parasitic copepods of the area. Dr. David Causey of the University of Arkansas also aided in the

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identification of parasitic copepods and Dr. Lloyd Shinners of Southern Methodist University identified the angiosperms of the area. Dr. George K. Reid, Jr. then of the Agricultural and Mechanical College of Texas gave many valuable suggestions and criticisms and all members of the Marine Division of the Texas Game and Fish Commission contributed information. Dr. Joel Hedgpeth, Dr. Carl L. Hubbs and other members of the Scripps Institution of Oceanography, University of California gave assistance in the preparation of the manuscript.

PREVIOUS INVESTIGATIONS

No previous investigation of this scope has been attempted. Pearson (1927) limited his work in the area to a basic life history study of the Sciaenid fishes. Hedgpeth (1947) contributed information concerning salinities, tidal exchange, fish production, pass cutting, and the probable ecological effect of a proposed earth fill causeway. Baker (1947) gave additional history of salinities in the area before the dredging of the Intracoastal Waterway. Gunter (1945) contributed a concise analysis of pass dredging in the area up to that time. Hedgpeth (1953) listed several organisms from the southern reaches of this hypersaline bay. Burr (1930) noted a sudden change in salinity in the lagoon. Collier and Hedgpeth (1950) compiled and brought up to date available information on the Laguna Madre.

DESCRIPTION OF AREAS—GENERAL

The Upper Laguna Madre is located on the Texas Gulf coast immediately south of Corpus Christi Bay (Figure 1). It is separated from the Gulf of Mexico by Padre Island, a link in the chain of barrier islands along the Texas coast, and from Corpus Christi Bay by a land fill causeway, the northern boundary of the survey area.

This long, narrow coastal lagoon is bisected imperfectly by the Intracoastal Waterway, which is 125 feet wide and 12 feet deep. Spoil banks from this canal form a dike 13 miles long effectively dividing the northern part of the bay. Beyond this point, spoil banks are staggered and the division is less effective. The terms "east side" and "west side" are used locally to designate those areas respectively east and west of the Intracoastal Waterway.

Three natural islands are found in the region. All are small, not over one mile long. Pita Island is located on the west side, about five miles southwest of the Corpus Christi-Padre Island Causeway. North Bird Island is located eight miles south of the causeway and South Bird Island is two miles south of North Bird Island. Thirty-five miles south of the causeway a large semidry bar extends across the bay and is bisected by the Intracoastal Waterway. Bullard (1942) suggests that at latitude 27° North the north bound clockwise Gulf current meets the south bound counter-clockwise current. Sediments dropped along the Gulf beach side of Padre Island have blown inland to fill the Laguna. The Intracoastal Waterway through this fill is known as the landcut and is the southern boundary of the survey area.

The entrance to Baffin Bay, which is five miles wide, is on the western side 21 miles south of the causeway. Width of the lagoon at mean low tide ranges from three miles to five miles. The northern end is restricted by the causeway, which has three openings totaling 1,500 feet at extreme high water, or about 900 feet at mean low tide. The southern end is restricted by a landfill to little more than the width of the Intracoastal Waterway.

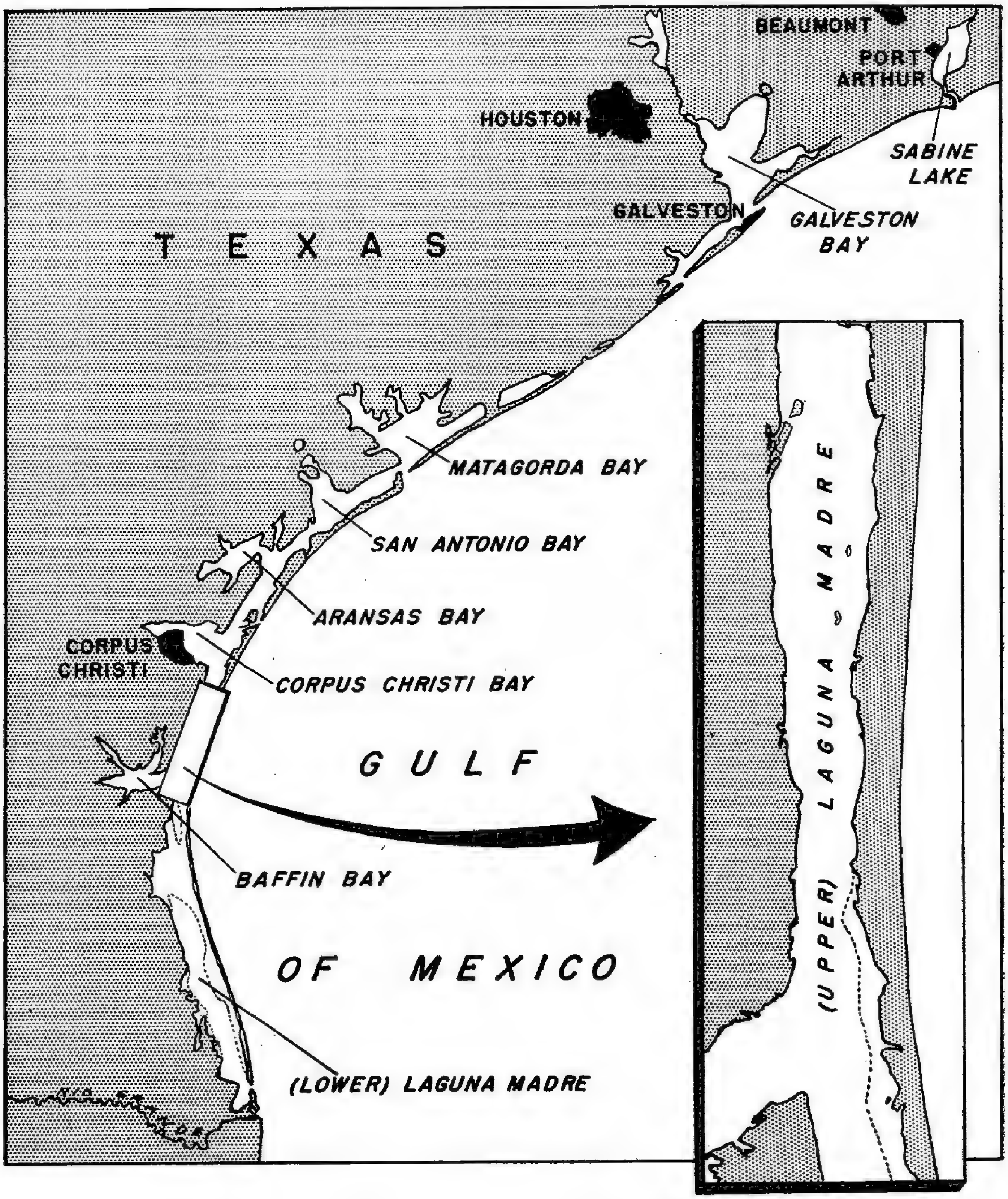
BEAUMONT
PORT ARTHUR
HOUSTON
SABINE LAKE
GALVESTON
GALVESTON BAY
TEXAS
MATAGORDA BAY
SAN ANTONIO BAY
ARANSAS BAY
CORPUS CHRISTI
CORPUS CHRISTI BAY
GULF OF MEXICO
BAFFIN BAY
(LOWER) LAGUNA MADRE
(UPPER) LAGUNA MADRE

Fig. 1. Map of the Texas Coast showing location of area studied.

DEPTHS AND STATIONS

Depths shown on most maps are not entirely accurate because mean low water is extremenly difficult to determine. Because of the lake-like character of the lagoon, each prevailing wind influences it in a manner similar to a seiche. However, the water movement is not rhythmic. In general the entire upper eight miles is very shallow. The western side gradually becomes deeper until another shallow bar is reached about five miles north of Baffin Bay and extending to Baffin Bay. The entrance to Baffin Bay is "rocky" and varies in depth from a few inches (on rocks) to twelve feet. South of Baffin Bay the water depth ranges from eight feet near Baffin Bay to three feet near the landcut.

Depths on the eastern side range from one to three feet for 13 miles south of the causeway where there is a natural basin five feet deep. South of this basin are mud flats, large bars of quartose sand and silt often barely covered with water. These flats extend southward about twelve miles. Near the site of old Yarborough Pass is another basin five miles long with depths to nine feet. South of this is landfill. Biological stations were established early in the survey (Figure 2).

HISTORY

The Laguna Madre has been the Texas bay least affected by man. From a position of little economic importance, however, it has risen to predominance, supplying over sixty per cent of the total state catch of bay fishes. Some interesting portions of its history concern efforts to open passes into the gulf, dredging of the Intracoastal Waterway, building of the Padre Island Causeway, effects of hurricanes, periodic fish mortality, and warfare between commercial and sports fishing interests.

It is possible that before 1919 the Laguna Madre extended for over 100 miles as an uninterrupted bay. Some siltation from Padre Island may already have been present in the bay. There is evidence that during the hurricane of that year a portion of Padre Island was moved into the water, effectively dividing the bay into two parts.

Sports fishing was probably restricted largely to the upper eight miles of the area until after World War II, when boats with outboard motors became more available. However, for many years sports fishermen and commercial fishermen have vied vocally for the water, each group feeling it has a right to complete control of the fishing.

At the present time legal commercial fishing in the northern Laguna Madre is restricted to trot lines, but illegal nets are often used under cover of darkness. "Sports-fishing" has increased many fold and the average catch is above that of any other Texas bay.[2]

In 1950, a landfill causeway was constructed from Encinal Peninsula to Padre Island. Three openings, each five hundred feet wide, were left from Corpus Christi Bay to the lagoon. One of these, near Padre Island, immediately filled with sand and is completely closed.

In 1948, the Intracoastal Waterway was completed. Through this canal moderate amounts of water from Corpus Christi Bay and the lower Laguna Madre enter the lagoon. This has reduced salinity below the lethal concentration of 80‰ and allowed an avenue of escape for fish, but has not completely solved the problem of hypersalinity.

The creeks of Los Olmos, Jabocillos, Petronilla and San Fernando empty silt into Baffin Bay and not into the lagoon proper. These creeks are dry except during the rainy season. Even then, light rainfall tends only to bring more salt in from banks. Burr (1930) reasoned that the lagoon freshened up during high tide near the Point of Rocks because fresh water seeped through the sand. In this survey it was found that the water often became more saline as high tides washed away salt deposits on the shore. Dr.

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[2] It should be explained, for the benefit of those unfamiliar with Texas custom that a significant part of the commercial catch of fishes from Texas bays is made by "sport" fishermen, who purchase the inexpensive commercial license (often *ex post facto*) and sell their catch to wholesalers. It is estimated that some 38% of the total catch of trout and redfish from the Corpus Christi area in 1953 was contributed from such hook and line "sport" fishing. Thus, in a real sense, the Laguna Madre is not closed to commercial fishing, but to net fishing only. Many "sport" fishermen do not feel that their trip has been a success unless they make expenses in this manner. (J. W. Hedgpeth.)

Gene A. Rusnak of the Scripps Institute of Oceanography in an oral communication stated that fresh water was present only a few inches below the surface one day after a heavy rain.

Geophysical survey crews have worked the entire area during the past four years. An existing channel from the Pure Oil Docks to the Intracoastal Canal has been redredged and the resulting spoil, covering about one square mile, has remained devoid of plant life for three years. Silt from dredging and oil well drilling in the vicinity of Yarborough Pass covered an area of approximately twenty-four square miles in 1953. Other siltation resulted from redredging of the Intracoastal Waterway, and siltation is evident along spoil banks south of the causeway. A new channel was dredged from Pita Island to the Intracoastal Waterway. Oil wells have been located near Yarborough Pass, at North Bird Island, the Pure Oil Channel and Pita Island.

Geologically speaking, the upper Laguna Madre is probably in its final stages of evolution. Evaporation is high, current flow is restricted, and no major streams flow into the area. Sand from Padre Island has displaced water in several instances.

Periodically a proposal is made by fishermen of the Corpus Christi-Kingsville area to cut passes through Padre Island linking the Laguna Madre with the Gulf, and several such passes have been opened. The principal pass or opening of interest is near Murdock's Landing and is called Yarborough Pass. Gunter (1945) give complete information on openings and closings of this pass from December 5, 1940 until December, 1944. A condensation of these data shows that every attempt ended in failure.

PASS OPENED	*PASS CLOSED*
April 14, 1941	September, 1941
November 9, 1942	April, 1943
May 16, 1944	Shortly thereafter
November 21, 1944	December, 1944

Thus during this period of thirty-two months the pass was opened four times, remained partially open for about ten months, and fully open about six months. It has been reported that during these openings water from the Gulf never entered the bay area more than one mile. Salinities were lowered less than one-half of one per cent in every case.

On February 14, 1952, this pass was again opened, 60 feet wide, into the Gulf. Three weeks later it was three feet wide. Dynamite was detonated in an effort to widen the stream but this failed. Extremely high tides two days later increased the water flow somewhat, but within three weeks this flow ceased completely.

In this last instance, water from the Gulf penetrated somewhat further into the bay, the most distant point being about twelve miles from the pass. This was determined by use of fluorescein dye in the water and by salinity checks. The increased distance was probably due to fairly rapid currents in the Intracoastal Waterway. Heavy rainfall in March, 1952, lowered salinities throughout the entire bay much more than did water from the pass. A total of twenty-one sciaenids, mostly black drum, were captured in nets which were stretched across the pass during the six weeks it was open.

FISH MORTALITY

Prior to 1948, fish mortality of two types occurred in this bay, mortality caused by hypersalinity, and more serious kills caused by sudden drops in water temperature.

Since the construction of the Intracoastal Waterway, kills from hypersalinity have been practically eliminated, primarily because fish are now able to leave the area. Kills from hypersalinity are known to have occurred in 1936, 1937, 1939, 1943, 1944, and 1945, and commercial fishermen speak of kills that occurred 20 and 30 years ago.

Mass mortalities from cold water commonly called "freezes" are a repeated event in the history of the Laguna Madre and have been very serious. Populations have recovered from these setbacks in about three years. Major freezes are said to occur about every 14 years, but severe freezes occurred in 1940, 1945, 1947, and 1951. On January 31, February 1, and February 2, of the latter year air temperature dropped to 18° F. Investigations of biologists of the Texas Game and Fish Commission showed that millions of pounds of fish were killed along the Texas coast, many in the Laguna Madre. All species suffered severely. One sea trout, forty-eight inches long and probably weighing about twenty-five pounds, was found dead near the Point of Rocks. In October and November, 1951, gill nets were set in the area. Only four fish were taken. In February, 1952, these same gill nets were catching over 100 black drum each night, evidently new fish from the Gulf or from other bays. By mid-winter of 1953, black drum were so abundant that fishing became difficult, the nets loading down with fish. In 1954, trout and redfish populations returned to normal.

RED WATERS

Discolored water, often present in the upper Laguna Madre, is usually spoken of as "red water" or "bad water." Actually the water may be reddish or yellowish or even brown. It is not muddy and is not exceptionally turbid as light transmission is normally about 92 per cent. This discolored water is commonly associated with high salinity but is not necessarily so. One form of discoloration, present in the Point of Rocks area, appears to originate in Baffin Bay. Pollution from the Celanese Corporation has often been suggested as the cause but a similar discoloration was observed before the plant was installed. Several factors are known to contribute to red waters elsewhere, and there are probably others. The possibilities are:

1. Dissolved iron compounds are usually found with high salinity. As evaporation increases, water becomes more dense, and sinks to the bottom causing iron compounds to mix with the water.
2. Decaying vegetation, not necessarily associated with hypersalinity, is abundant in areas of poor circulation. Reddish chromatophores in the vegetation break down, giving the water a brownish appearance.
3. Phytoplankton—Certain dinoflagellates are sometimes present in abundance. These give the water a yellowish cast.
4. Clay deposits in Baffin Bay may be a causative factor.

Physical Characteristics

SHORE FEATURES AND WATERSHED

Padre Island is a long and narrow sand "barrier" island characterized by unstable dunes and shifting shorelines. There are indications that this shoreline has been constantly encroaching on the water area. The western shoreline or mainland, is noted for sparse, semiarid type vegetation and by a lack of any marsh areas. Tide pools are common but are shallow and temporary. No true rock was located although hard accumulations of small shell are abundant. The Point of Rocks, twenty-one miles south of the causeway, consists of small shell accumulations and masses of serpulid worm tubes and barnacles. Beachrock is found across Baffin Bay along the western shoreline, near the Intracoastal Waterway south of Baffin Bay, and at scattered points north of Baffin Bay along the western shore. One group of beachrock known as the "Little Point of Rock" is located about eight miles north of Baffin Bay.

The land cut is characterized by blowing sand and by gypsum rosettes on the spoils.

Quartose sand is present throughout the area, but near the Point of Rocks some of the sand is calcareous material. Vegetation is thick on the northern flats; the mid-area is devoid of vegetation, and mud is present near the land cut (Figure 3). Masses of dead vegetation are found along the upper shoreline, blown by the wind into rolls.

The major watershed for this area is around the Baffin Bay region and is about twenty miles from the lagoon proper. Breuer (1952) reported as much as eighteen feet of unconsolidated material at points in Baffin Bay. Padre Island is of little value as a watershed; the dry sands soak up water rapidly. The western shore is little better, for the slope of the land is very gradual although the soil is not as porous as that of Padre Island.

BOTTOM TYPES

Figure 2 show the biological stations established according to bottom types. Table 1 lists these types. Some changes caused by beach drift and siltation are noted.

TABLE 1

Bottom Types

Station	Depth	Type Bottom	Vegetation*
25A	3–5 ft.	Sand, Silt, Shell	(1) *Diplanthera wrightii* Aschers (2) *Acetabularia crenulata* Lamarck
26	2–4 ft.	Sand, Silt, Mud, Shell	Both plus (3) *Ruppia maritima* Aschers
27	4–6 ft.	Sand, Silt, Mud, Dead Shell	(1) *D. wrightii* (sparce)
28	1–3 ft.	Shell, Sand, Silt	All three
29	2–5 ft.	Hard Sand, Dead Shell	All three
30	4–6 ft.	Hard Sand, Dead Shell	*Diplanthera wrightii* Aschers
31	1–4 ft.	Dead Shell, Loose Sand, Silt	*Diplanthera wrightii* Aschers
32	3–5 ft.	Clay, Shell, Rock	None
33		Eliminated	
34	5–8 ft.	Small Rocks, Sand	None
35	5–9 ft.	Silt, Sand (silted badly)	None
36	7–9 ft.	Silt, Sand, Rock (silted)	None
37	.5–3.5 ft.	Loose Sand, Rock, Silt	*Acetabularia crenulata* Lamarck *Diplanthera wrightii* Aschers

* Vegetation varies each year.

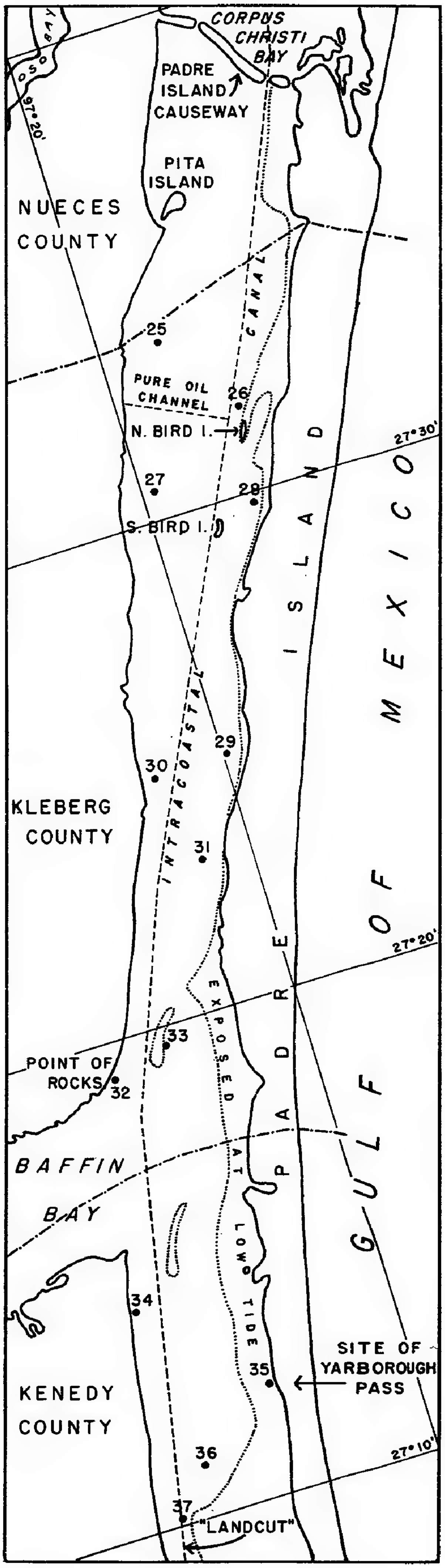
OSO BAY
97°20'
CORPUS CHRISTI BAY
PADRE ISLAND CAUSEWAY
PITA ISLAND
NUECES COUNTY
25
PURE OIL CHANNEL
26
N. BIRD I.
27
28
S. BIRD I.
27°30'
INTRACOASTAL CANAL
PADRE ISLAND
GULF OF MEXICO
29
30
KLEBERG COUNTY
31
27°20'
EXPOSED AT LOW TIDE
33
POINT OF ROCKS
32
BAFFIN BAY
34
KENEDY COUNTY
35
SITE OF YARBOROUGH PASS
36
27°10'
37
"LANDCUT"

Fig. 2. Station locations and descriptive features in the upper Laguna Madre.

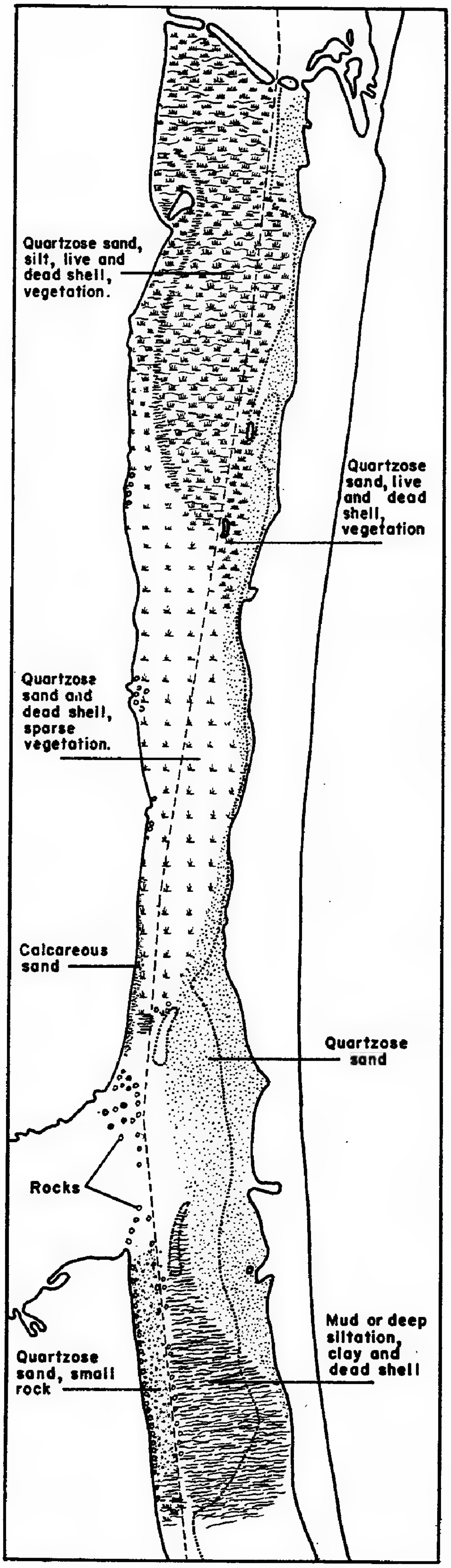
Quartzose sand, silt, live and dead shell, vegetation.
Quartzose sand, live and dead shell, vegetation
Quartzose sand and dead shell, sparse vegetation.
Calcareous sand
Quartzose sand
Rocks
Mud or deep siltation, clay and dead shell
Quartzose sand, small rock

Fig. 3. Bottom types in the upper Laguna Madre.

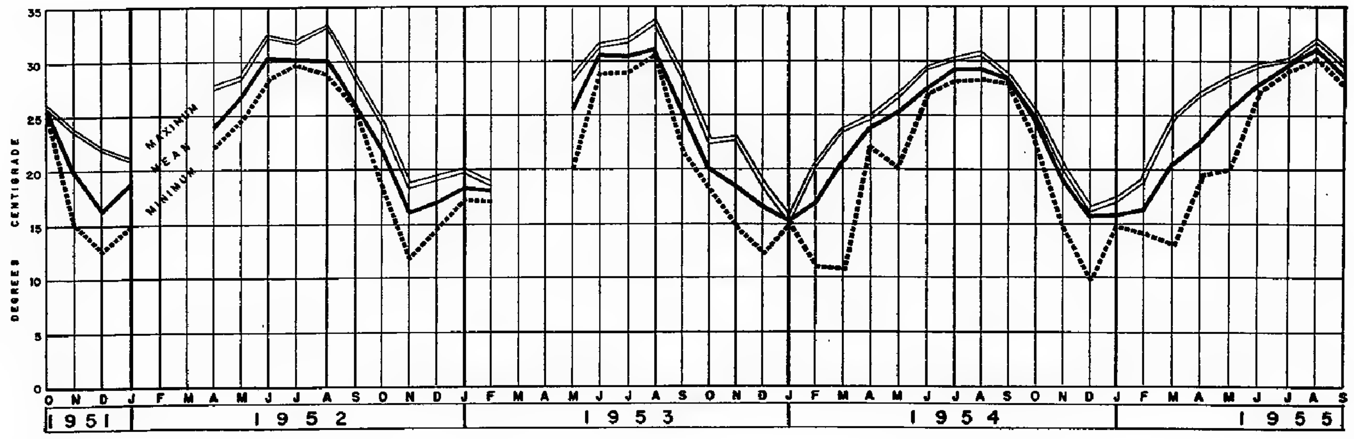

FIG. 4. Maximum, minimum, and mean bottom temperatures by month for twelve stations in the upper Laguna Madre.

HYDROGRAPHY

Temperature—Bottom water temperature varied over a four-year period from 4° to 35° Centigrade (Figure 4). Because of the shallow nature of this bay, changes in water temperature occur rapidly and there is little variation between bottom and surface temperature.

Water temperature is of primary importance to marine life because it affects feeding activities, regulates spawning to a large degree, and is a definite factor in determining salinity tolerance. Average or mean temperatures are of value to this survey when considered on a large scale over a period of years (Table 2). Consideration must be given, however, to local climatic factors which caused these temperatures to vary greatly in a single month. These figures represent samples taken twice each month from twelve stations whenever possible. Temperatures of 35° and 44° were recorded at Station 33, a station which was later discontinued.

Because about four hours were required to sample the upper lagoon and water temperature varied as much as four degrees in that length of time, no attempt was made to include isotherms. However, one noteworthy "cold spot" is located near the sulphur well at Yarborough Pass, where the bottom temperature is normally one degree at variance from a station two miles away. Temperatures in the deeper southern end of the area vary much less than in the shallow northern end.

Salinity—Considerable interest has been shown in the excessive salinity of the upper Laguna Madre. Hedgpeth (1953) indicated that the highest salinity recorded between 1946 and 1948 was 113.9‰ and that salinities above 70‰ were not uncommon. A low salinity of 17.9‰ was noted near Pita Island by Baker (1948) who also listed several salinities above 100‰ but these were probably in Baffin Bay, not in the upper lagoon. For a comparison of some salinities before and after the construction of the Intracoastal Waterway in 1948, selective samples of Baker's reports are used together with readings of a later date (Table 3). All of Baker's work was done before completion of this canal. All stations were sampled at least once each month and several stations were sampled more than ten times each month. The Mohr method and the hydrometer method were both used to analyze samples. See Figure 1 for station locations. Surface and bottom samples were obtained until it was noted that variation between these two was negligible.

Periods for which salinities are not given resulted from mechanical failure or concentration of effort in other areas (usually Yarborough Pass).

It would appear that dredging of the Intracoastal Waterway has modified salinities in the Upper Laguna Madre but has not been as effective in lowering salinities as was predicted. Salinity has neither risen above 80‰, in the lagoon nor in Baffin Bay (where 100‰ was not uncommon), nor have waters of very low salinity remained in the area any length of time. The region particularly modified was that portion near Baffin Bay.

TABLE 2

Water Temperature (Centrigrade)

Date		Maximum	Minimum	Mean
1951	October	26.3	25.7	26.1
	November	23.8	15.4	18.2
	December	22.1	12.7	16.2
1952	January	21.0	14.9	18.8
	February	Insufficient Data		
	March	Insufficient Data		
	April	27.6	22.1	24.0
	May	28.3	24.6	26.6
	June	32.5	28.2	30.4
	July	31.8	29.6	30.2
	August	33.2	28.7	30.1
	September	28.5	25.7	25.9
	October	24.5	18.5	22.9
	November	18.5	12.0	16.0
	December	19.3	14.8	16.8
1953	January	19.9	17.1	18.1
	February	18.8	17.1	18.0
	March			
	April			
	May	28.3	19.8	25.4
	June	32.6	28.9	30.6
	July	32.0	28.8	30.4
	August	33.5	30.5	31.0
	September	29.0	22.0	25.5
	October	22.6	18.4	20.0
	November	22.8	14.9	18.5
	December	18.5	12.5	16.5
1954	January	15.4	15.2	15.4
	February	20.6	11.1	17.0
	March	24.0	10.8	20.6
	April	24.8	22.2	23.9
	May	26.8	20.1	25.4
	June	29.4	26.7	27.5
	July	30.0	28.0	29.1
	August	30.6	28.1	29.1
	September	28.7	27.9	28.4
	October	25.4	22.8	24.2
	November	20.1	17.0	18.9
	December	16.5	9.9	15.6
1955	January	17.1	14.7	15.7
	February	19.1	14.2	16.3
	March	24.8	13.1	20.2
	April	27.0	19.1	22.6
	May	28.5	20.0	25.5
	June	29.6	27.0	27.6
	July	30.1	29.0	29.5
	August	32.0	30.3	31.2
	September	29.6	27.7	28.5

TABLE 3

Comparison of Monthly Salinities Before and After Completion of Intracoastal Waterway in 1948

Date	Station 25	Station 28	Station 32
January, 1948	69.0	36.3	52.7
January, 1952	37.6	38.7	......
January, 1953	48.0	50.5	51.5
January, 1955	48.5	45.0	58.1
February, 1942	......	.	31.4
February, 1947	27.2	27.2	47.2
February, 1952	......	......	50.0
May, 1941	51.6	51.2	36.4
May, 1947	32.3	42.6	57.1
May, 1952	49.0	50.3	55.5
May, 1953	50.8	51.5	......
May, 1954	36.5	43.5	50.5
June, 1944	26.3	23.5	27.0
June, 1947	33.6	41.0	66.6
June, 1948	60.8	60.8	72.4
June, 1952	50.7	61.5	55.9
June, 1953	68.8	66.2	66.5
June, 1954	46.5	49.6	49.6
June, 1955	57.8	57.9	57.2
July, 1946	40.0	75.4	78.8
July, 1947	39.8	62.0	71.8
July, 1948	64.6	69.5	78.4
July, 1952	58.3	53.2	56.0
July, 1953			
July, 1954	49.1	48.1	50.5
July, 1955	62.7	58.7	57.4
August, 1946	36.6	54.4	80.0
August, 1947	32.1	32.9	62.0
August, 1948	56.0	59.5	66.1
August, 1952			
August, 1953	76.4	79.2	76.5
August, 1954	54.7	54.1	52.0
August, 1955	65.6	64.0	61.4
September, 1946	35.1	37.3	70.8
September, 1947	54.4	62.4	69.3
September, 1948	50.2	56.5	62.4
September, 1953	53.0	Heavy Rainfall	
September, 1954			
September, 1955	44.0	49.0	43.4
October, 1946	32.7	39.9	32.7
October, 1947	38.0	49.1	38.0
October, 1948	42.2	49.2	42.2
October, 1951	39.0	41.5	39.8
October, 1952			
October, 1953	47.0	49.0	52.3
October, 1954	45.0	47.0	55.0
October, 1955	38.5	40.5	35.2
November, 1946	23.2	23.7	50.7
November, 1947	34.2	34.2	54.7
November, 1951	35.9	36.8	37.3
November, 1952			
November, 1953	42.0	41.6	52.7
November, 1954	44.1	46.8	51.2
November, 1955	37.0	37.0	35.5
December, 1946	22.1	31.2	46.8
December, 1947	54.7	32.4	57.9
December, 1951	38.2	38.0	......
December, 1952			
December, 1953	40.2	45.2	......
December, 1954	48.5	......	59.0
December, 1955	36.1	36.6	36.5

The upper areas, however, were often less saline prior to dredging of the canal and to building of the earthfill causeway. The influence of the canal is usually noted in July and August.

Average salinity for individual stations of this survey with most samples included is presented in Table 4.

Water of high salinity acted as a buffer against less saline water entering the lagoon from either end. Mixing of these waters of different densities was extremely slow, and a definite line of demarcation was usually present. This block of highly saline water pushed ahead of the fresher water often with a layer of fresher water over the surface. When the highly saline water reached either the causeway or the landcut, it piled up; and literally bounced back against the fresher water. This saline block moved toward the north or south end according to wind direction (Figure 5).

Figure 6 shows the maximum, minimum, and mean salinities by month for the composite stations of the upper lagoon.

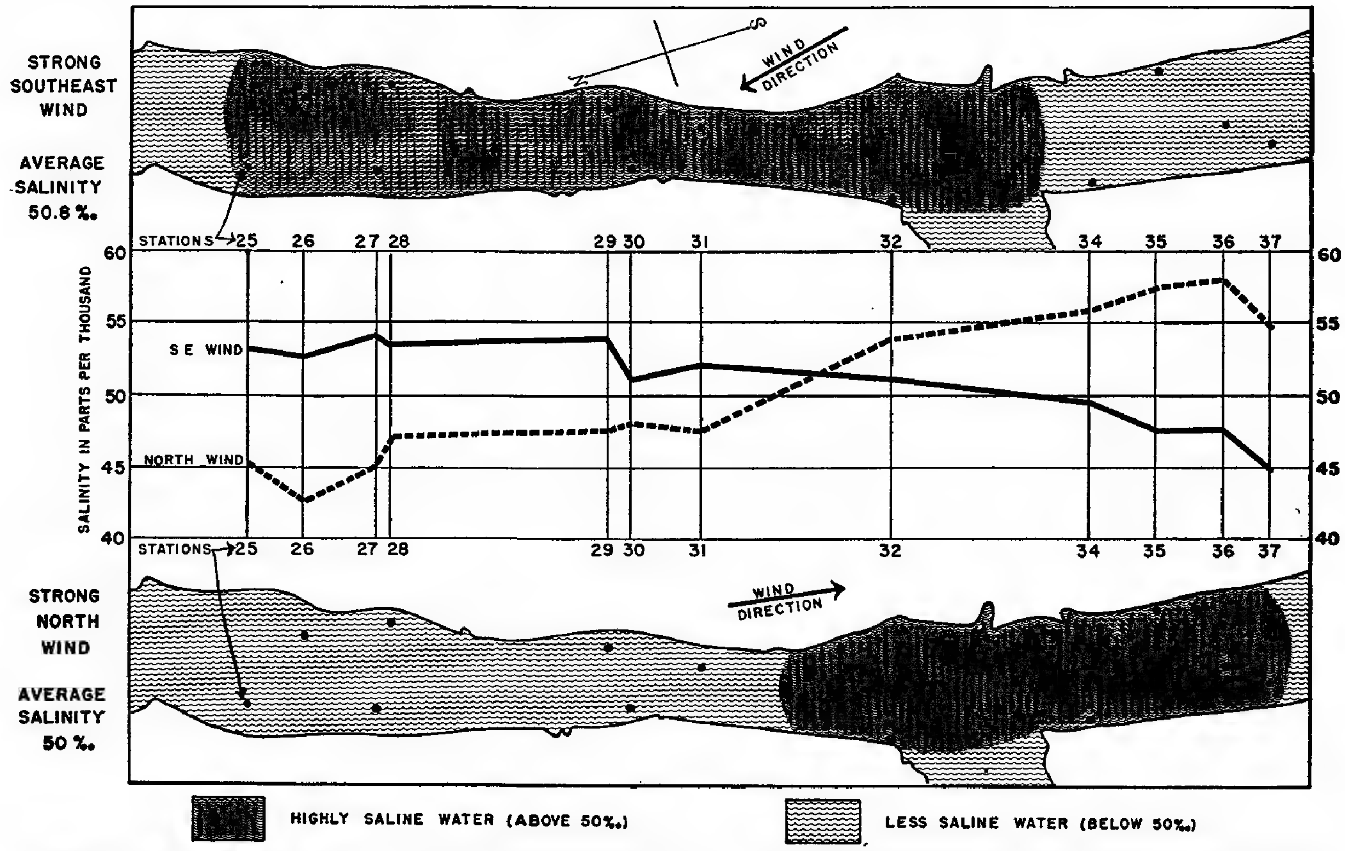
STRONG SOUTHEAST WIND
AVERAGE SALINITY 50.8 ‰
N
WIND DIRECTION
STATIONS 25 26 27 28 29 30 31 32 34 35 36 37
60
55
50
45
40
SALINITY IN PARTS PER THOUSAND
S E WIND
NORTH WIND
STATIONS 25 26 27 28 29 30 31 32 34 35 36 37
STRONG NORTH WIND
AVERAGE SALINITY 50 ‰
WIND DIRECTION
HIGHLY SALINE WATER (ABOVE 50‰)
LESS SALINE WATER (BELOW 50‰)

FIG. 5. Diagram showing movement of salinity block with prevailing wind tide, and corresponding graph showing salinities at each station during southeast and north winds.

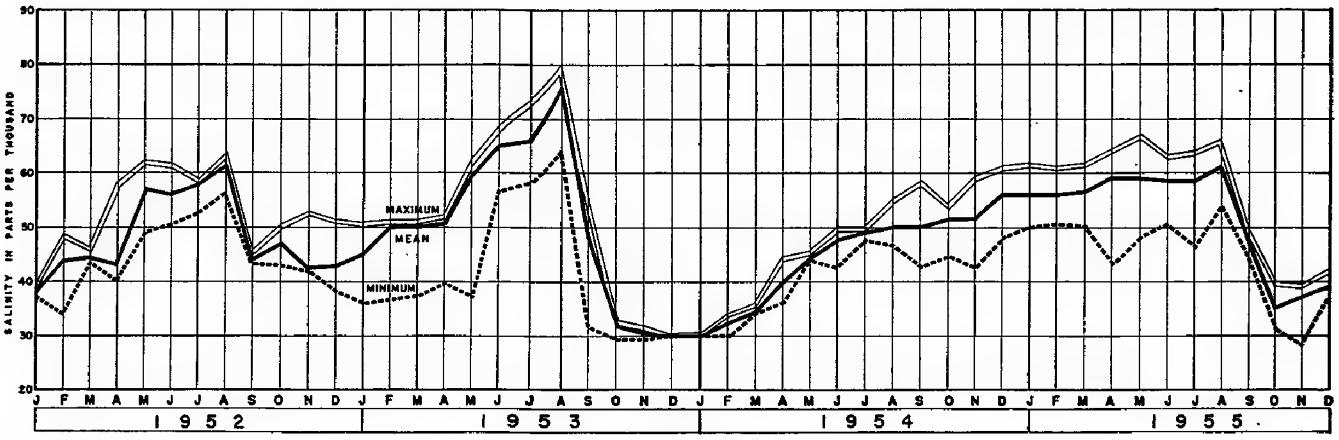

FIG. 6. Maximum, minimum, and mean salinity by month for twelve stations in the upper Laguna Madre.

TABLE 4

Average Salinity Expressed in ‰, Upper Laguna Madre

Date	Station												
	25	26	27	28	29	30	31	32	34	35	36	37	
October, 1951	39.0	......	39.6	41.5	......	38.0	39.9	39.8	......	......	......	......	
November, 1951	......	37.0	35.9	36.8	36.0	36.9	36.9	37.3	......	37.4	37.6	......	
December, 1951	......	35.8	38.2	37.3	......	......	......	......	......	37.2	......	36.0	
January, 1952	38.0	38.5	38.4	39.0	......	......	......	......	......	......	......	......	
February, 1952	......	......	......	......	......	......	......	......	42.5	42.0	42.0	47.5	
March, 1952	......	......	......	......	......	......	......	......	44.2	44.0	44.9	45.0	
April, 1952	40.6	40.6	42.9	......	50.0	49.2	57.6	......	......	......	......	......	
May, 1952	48.4	57.1	48.8	50.1	......	......	......	55.9	61.2	62.3	......	......	
June, 1952	58.0	53.5	57.5	55.4	53.3	50.9	50.8	50.0	......	......	......	......	
July, 1952	58.3	56.0	58.1	57.2	56.3	58.6	57.1	56.0	52.3	54.9	54.2	52.5	
August, 1952	69.0	59.1	61.8	60.0	......	......	......	......	......	......	......	......	
September, 1952	45.3	45.4	45.3	......	......	......	44.0	44.5	......	......	......	......	
October, 1952	45.0	44.5	45.6	48.1	50.0	52.3	49.9	......	......	......	......	......	
November, 1952	42.1	47.8	43.0	49.2	......	......	......	......	......	......	......	......	
December, 1952	40.0	45.5	39.2	45.0	......	......	......	......	......	......	......	......	
January, 1953	45.5	48.9	39.1	48.5	......	......	......	......	......	......	......	......	
February, 1953	......	......	......	......	......	......	......	......	......	......	......	......	
March, 1953	......	......	......	......	......	......	......	......	......	......	......	......	
April, 1953	......	......	......	......	......	......	......	......	......	......	......	......	
May, 1953	50.8	37.1	50.7	50.3	50.6	50.8	51.0	......	......	......	......	......	
June, 1953	60.5	61.0	66.2	61.7	61.2	61.5	68.1	55.5	62.0	63.8	59.4	56.1	
July, 1953	......	......	......	......	......	......	......	......	......	......	......	......	
August, 1953	76.4	72.4	77.0	79.2	73.0	74.5	76.0	......	......	......	......	......	
September, 1953	33.0	37.5	47.5	35.4	35.0	33.0	32.1	......	......	......	......	......	Heavy Rainfall
October, 1953	32.4	27.3	31.0	32.5	32.5	33.0	30.5	......	......	......	......	......	
November, 1953	30.5	29.9	31.0	31.0	33.5	......	......	......	......	......	......	......	
December, 1953	29.0	29.8	31.0	30.0	29.5	30.0	29.0	......	......	......	......	......	

TABLE 4—Continued

Average Salinity Expressed in ‰, Upper Laguna Madre

Date	Station												
	25	26	27	28	29	30	31	32	34	35	36	37	
January, 1954	32.5	30.3	31.5	31.4	32.0	31.8	......	......	......	......	......	......	
February, 1954	33.0	34.5	33.2	34.0	34.1	35.0	33.0	......	......	......	......	......	
March, 1954	33.5	34.5	35.0	35.1	35.0	36.0	37.0	......	......	......	......	......	
April, 1954	36.5	43.0	36.5	42.5	43.0	43.0	44.0	......	......	......	......	......	
May, 1954	44.6	45.0	47.0	47.0	46.8	46.5	47.0	......	......	......	......	......	
June, 1954	46.5	48.0	46.0	47.1	46.8	46.3	49.2	45.9	44.4	44.2	44.3	48.0	Cut 45.9
July, 1954	49.1	49.6	47.6	48.1	48.5	46.8	49.8	46.5	46.0	47.0	45.8	46.0	
August, 1954	52.0	51.1	48.6	52.2	52.2	52.0	51.8	49.0	48.8	49.6	47.7	47.5	
September, 1954	45.0	42.5	45.0	47.0	47.2	48.0	47.4	54.5	56.0	57.2	58.0	54.8	Fall Tide
October, 1954	53.0	52.4	54.0	53.4	53.6	51.0	52.3	51.3	49.8	47.6	47.8	44.6	S. E. Wind
November, 1954	44.1	42.2	45.6	46.8	30.4	52.2	51.2	54.0	......	56.4	59.6	53.0	North Wind
December, 1954	48.9	51.4	52.0	56.5	58.1	59.0	60.1	59.2	57.0	60.9	59.6	55.0	
January, 1955	38.2	56.4	42.8	45.0	53.2	52.0	54.6	58.1	60.0	60.4	59.9	59.1	
February, 1955	......	......	......	......	......	......	......	......	......	......	......	......	
March, 1955	......	......	......	......	......	......	......	......	......	......	......	......	
April, 1955	64.0	55.0	64.0	55.0	63.0	64.0	64.0	60.0	52.0	57.0	58.0	56.0	
May, 1955	......	......	......	......	......	......	......	......	......	......	......	......	
June, 1955	......	......	......	......	......	......	......	......	......	......	......	......	
July, 1955	62.7	58.9	63.3	58.7	58.4	57.8	57.6	57.4	52.0	51.0	51.7	46.8	Mk. 181 46.5
August, 1955	65.6	65.0	63.4	64.0	64.0	62.0	61.5	61.4	57.4	57.4	56.0	54.0	
September, 1955	44.6	47.4	47.5	49.0	46.4	47.0	46.4	43.4	41.0	45.0	45.4	46.0	Rain
October, 1955	35.6	30.1	33.1	30.8	31.0	31.8	32.0	30.0	33.0	35.0	34.5	33.5	
November, 1955	37.5	37.0	38.0	37.5	38.0	38.0	39.1	36.5	35.0	35.5	35.0	34.0	
December, 1955	......	......	......	......	......	......	......	......	......	......	......	......	

Other Chemical Characteristics—Only in the boat basins has any problem of oxygen deficiency or excessive decomposition been encountered. A certain amount of noxious gases was present in piles of decaying vegetation, but the thorough mixing of water in these regions nullified any adverse effects. Pollution of a chemical nature was not observed although Baffin Bay in the past has been the scene of spillage from chemical plants in the watershed area.

Hedgpeth (1953) compiled a comparison between normal sea water and water of Baffin Bay. In some respects the lagoon was chemically deficient at that time of analysis.

Substance	Sea Water	Laguna Madre	Laguna Madre Per Cent of Sea Water
Cl	55.04%	60.50%	109.8%
SO_4	7.68	2.15	28.0
CO_3 (as HCO_3)	0.41	0.23	56.1
Na	30.62	31.40	102.2
K	1.19	N.D.	N.D.
Ca	1.15	0.93	80.9
Mg	3.69	3.68	99.9
‰	35.00	64.05	183.0

Nutrient concentrations were low possibly due to lack of an adequate watershed. As a comparison, portions of the lower Laguna Madre with its more normal water supply had a higher concentration of PO_4 (inorganic phosphorus concentration in microgram atoms PO_4—P per liter) and NO_2, NO_3 (Nitrite—Nitrate concentrations in microgram atoms N/liter).

		Unpublished Data of J. P. Breuer	
	1955 Upper Laguna Madre Area	1955 Lower Laguna Madre Area	Arroyo Colorado
Average PO_4	0.36	0.84	1.55
Average NO_2, NO_3	1.53	1.39	34.50

In spite of these factors the upper lagoon probably produced more food in the form of mullet and copepods per area than other Texas bays.

Meteorology—A calm day in the area under study was a rarity. Winds from the southeast or south-southeast are prevalent even during some winter months. However, when all northerly winds were grouped under one heading they were prevalent during winter months according to records of the Corpus Christi weather station (Table 5).

At least one period of very high wind occurred each month. Wind speed and direction is important in that it affects movement of marine organisms, movement of water and of the saline block, and is at times destructive to vegetation.

Wind and tidal action are interrelated in the upper Laguna Madre. Northerly winds bring in water from Corpus Christi Bay, lower the tide at the northern section, and raise the tide at the landcut by as much as one foot. Southeast winds have a reverse effect as do east winds. Strong west winds tend to have an effect similar to northerly winds. One sudden west wind of 50 miles per hour lowered the water level near North Bird Island 18 inches in less than one hour.

Spring and autumn high tides enter the area several days after they enter Corpus Christi Bay. The tidal level is raised about 16 inches but mixing is negligible and the tidal prism recedes virtually intact. These high tides usually occurred in March or April and in August or September.

Currents have not been completely plotted for the area. Drift cards were not very effective and the use of dyes was not practical over long periods. Reverse currents were

Table 5

Prevailing Winds

Month	Direction	Speed (mph)	Per Cent	Maximum Wind	
				Direction	Speed (mph)
October, 1951	S.E.	10.3	26	S.	30
November, 1951	S.E.	13.1	47	N.	46
December, 1951	S.S.E.	13.0	32	N.	36
January, 1952	S.S.E.	14.0	52	S.	34
February, 1952	S.S.E.	14.4	28	N.W.	42
March, 1952	E.	15.5	29	N.W.	49
April, 1952	S.E.	14.0	30	N.	37
May, 1952	S.E.	12.8	32	W.	50
June, 1952	S.E.	12.8	47	S.E.	28
July, 1952	S.S.E.	10.3	32	S.	40
August, 1952	S.S.E.	12.3	32	S.E.	27
September, 1952	E.	9.2	37	N.	32
October, 1952	N.E. & S.E.	8.9	----	N.	28
November, 1952	S.S.E.	13.0	27	N.	38
December, 1952	N.N.W.	11.5	28	N.	36
January, 1953	S.S.E.	13.2	32	N.W.	43
February, 1953	N.N.E.	13.3	30	S.	41
March, 1953	S.E.	14.0	39	S.	45
April, 1953	S.S.E.	14.3	33	S.	43
May, 1953	S.E.	14.6	35	N.	35
June, 1953	S.E.	12.5	47	S.E.	27
July, 1953	S.E.	12.5	42	S.E.	30
August, 1953	S.S.E.	10.4	32	S.E.	31
September, 1953		9.1	. .	N.	35
October, 1953	S.E.	9.9	29	N.W.	35
November,1953	N.N.E.	10.7	29	N.	29
December,1953	N.N.W.	13.0	26	N.W.	35
January, 1954	S.S.E.	12.9	29	S.E.	37
February, 1954	S.S.E.	12.8	28	N.	38
March, 1954	S.S.E.	15.8	32	S.E.	41
April, 1954	S.E.	14.6	45	S.E.	34
May, 1954	S.E.	13.0	42	N.	34
June, 1954	S.E.	14.0	63	S.E.	40
July, 1954	S.S.E.	12.3	61	S.E.	34
August, 1954	S.E.	12.5	32	S.E.	33
September, 1954	E.	9.9	53	E.	30
October, 1954	S.E.	10.4	19	N.	46
November, 1954	N.N.E.	11.6	43	S.	29
December, 1954	N.N.W.	12.1	42	S.	40
January, 1955	S.S.E.	13.4	23	N.W.	40
February, 1955	S.S.E.	16.2	28	N.	41
March, 1955	S.S.E.	17.0	45	N.	42
April, 1955	S.E.	15.9	43	S.E.	36
May, 1955	S.E.	14.9	55	S.	38
June, 1955	E.S.E.	11.4	40	S.	35
July, 1955	E.S.E.	11.4	35	S.	35
August, 1955	E.S.E.	9.4	42	S.E.	30
September, 1955	E.	9.5	30	N.E.	31
October, 1955	E.	8.5	23	N.	46
November, 1955		12.2	. .	N.	34
December, 1955	N.	9.0	42	N.	27

present in the upper area and less sharply defined near the landcut. A turning under and reversing of the current in the Intracoastal Canal sometimes took place near Marker 75. Current from Baffin Bay was governed by wind direction (Figures 7 and 8).

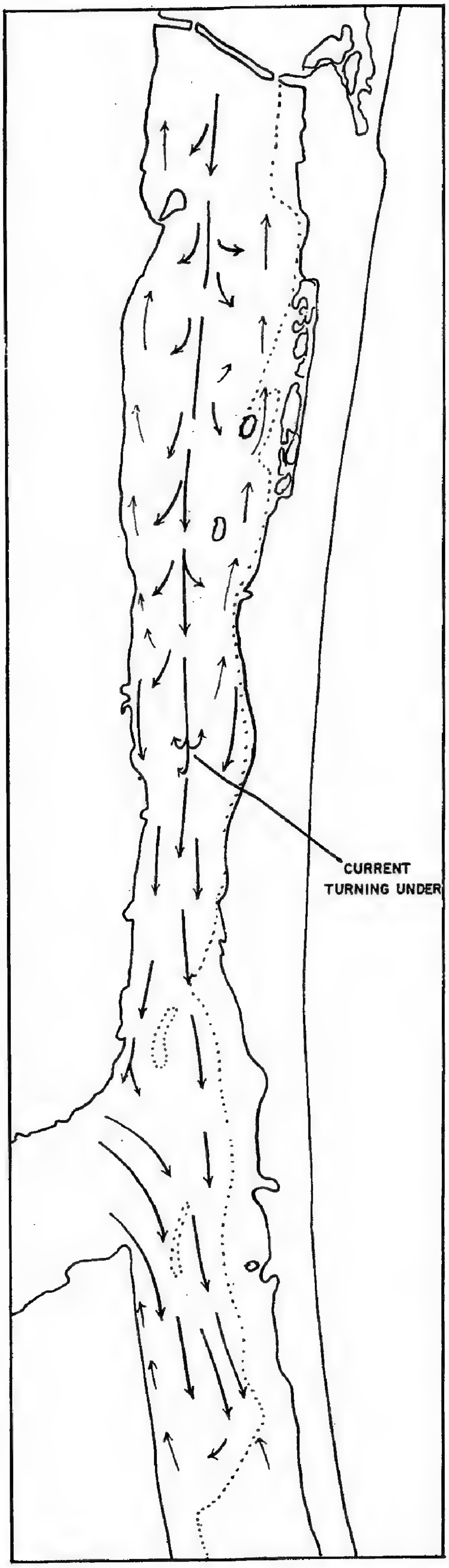
CURRENT
TURNING UNDER

Fig. 7. Currents flowing during north winds.

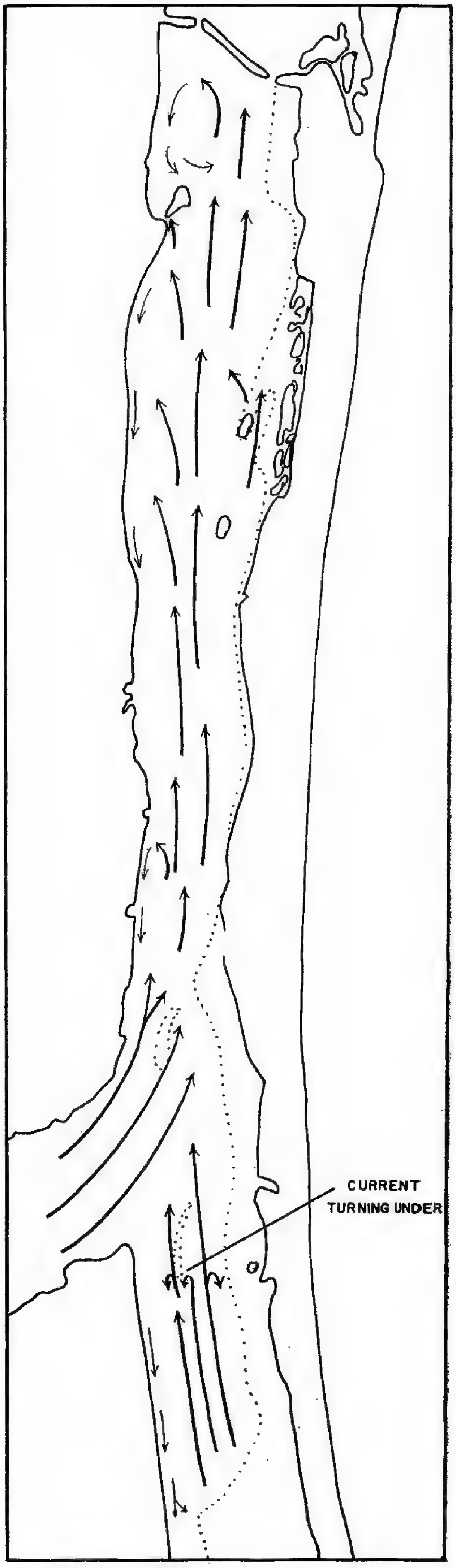
CURRENT
TURNING UNDER

Fig. 8. Currents flowing during south winds.

Rainfall—Rainfall has been of particular importance to the Laguna Madre, possibly more so than to any other Texas bay. The upper lagoon lies in two climatic zones. North of Baffin Bay is sub-humid; south of that point is semi-arid. In normal years in the semi-humid zone rainfall is greater than evaporation; in the semi-arid zone the reverse is true. During four years of the survey only sporadic torrential rainfall in September and October kept the entire area from becoming semi-arid. Rainfall on the upper watershed usually correlated well with salinity (Figure 9).

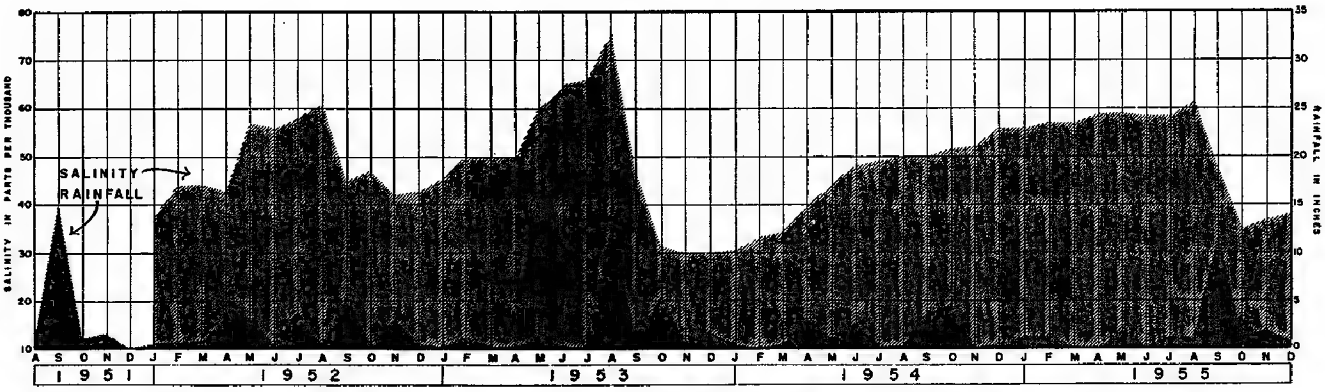

FIG. 9. Average salinity correlated with rainfall in the Flour Bluff area.

Biological Components

An effort was made to collect, identify and evaluate as many organisms as possible. Distribution, both seasonal and as otherwise governed by hydrographical and meteorological factors, was determined whenever feasible and a quantitative analysis was attempted in many cases.

Plankton was obtained with a one-meter 80 mesh net, pulled for five minutes at four miles per hour. Each station was sampled once each month. Samples were analyzed after preservation in five percent formalin and random samples were analyzed in the field without preservation. Samples were obtained from all levels by use of weights on the plankton tow.

One set of samples was analyzed using milipore filter mounts. This method was more useful in obtaining phytoplankton. Some invertebrates were obtained with push nets, minnow seines, dredges, and by hand from rocks and submerged pilings.

Vertebrates were obtained by push nets, dip nets, 20 to 100 foot minnow seines, two and one-half to seven inch stretch gill nets, trammel nets, otter trawls, pole and line, and by hand.

PHYTOPLANKTON

ORDER CENTRALES

Family Coscinodisaceae

Coscinodiscus asteromphalus Ehrenberg

Coscinodiscus radiatus Ehrenberg—This and the preceding species were obtained during period of unusually low salinity (29–33‰). They are not present in the area as a rule.

Thalassiosira sp.

Skeletonema sp.—This and the preceding species were found in limited number in salinities up to 45‰.

Stephanopyxis palmeriana (Greville) Grunow—This plankton collected on three occasions in the area near the landcut was not abundant.

Melosira sulcata (Ehrenberg) Kutzing

Melosira moniliformis (Muller) Agardh—These two species of *Melosira* were found at all the stations during spring and summer months, but were never abundant.

Family Soleniaceae

Rhizosolenia acuminata (H. Peragallo) Granville

Rhizosolenia alata Brightwell

Rhizosolenia imbricata Brightwell

Rhizosolenia setigera Brightwell—This was the most commonly collected species of this genus.

Family Chaetoceraceae

Chaetoceros sp.—This genus was not common.

Family Biddulphiaceae

Biddulphia mobiliensis Bailey—This was rare in the area.

ORDER PENNALES

Family Nitzchiaceae

Nitzschia seriata Cleve

Nitzschia longissima (Brebisson) Ralfs

Nitzschia closterium (Ehrenberg) W. Smith—The latter two species were fairly common in salinities of 40–45‰.

Family Naviculaceae

Pleurosigma angulatum W. Smith—This very comon form was collected in water up to 65‰ and was the most common phytoplankton.

Gyrosigma balticum W. Smith—This species was very common.

Navicula sp.—These were very common in salinity up to 60‰.

Family Fragillariaceae

Thalassiothrix sp.—Several species were present but not at all times and were never abundant.

Thalassionema nitzschioides Grunow—This was not common.

Synedra superba Kutzing—This was commonly collected in water of 30–50‰ salinity. It was the major representative of the family in the Laguna Madre.

PHYLUM SCHIZOPHYTA

CLASS CHLOROPHYCEAE

Family Dasycladaceae

Acetabularia crenulata Lamarck—This green algae was very common whenever salinities were between 30‰ and 50‰ and was always found attached to shell, rock or to wood particles. It tolerated salinities to 60‰ but was easily destroyed by combinations of high salinity and high temperature. Very little calcium deposition was noted in this area.

PHYLUM SPERMATOPHYTA

CLASS ANGIOSPERMAE

Family Zosteraceae

Diplanthera wrightii (Ascherson) Ascherson—Shoalgrass was the most abundant "grass" of the upper Laguna Madre. It was tolerant of high salinity and was virtually the only attached vegetation present at salinities above 45‰. Under optimum conditions there were as many as 3,600 emergent stems per square foot. This species was present at salinities of 1‰ and at 60‰ although some dwarfing occurred at high salinities.

Syringodium filiforme Kützing was scattered sparsely in the extreme upper lagoon in seasons of low salinity.

Family Potamogetinaceae

Ruppia maritima Linneaus—Widgeongrass was found in areas with salinities below 45‰ and was normally located near the edges of canals or in sheltered coves with silty bottom. Its growth was very dense in those areas. It was very important to marine life serving as spawning and nursery grounds for several species.

INVERTEBRATES

PHYLUM PROTOZOA

CLASS MASTIGOPHORA

Order Dinoflagellidia

Ceratium tripos (O. F. Müller) Nitzsch—*Ceratium fusus* (Ehr.) Du Jardin—Both of these species were rare and were not foun din high salinity over 40‰.

PHYLUM PORIFERA

Two unidentified forms have been orally reported by D. W. Miles, formerly of the Texas Game and Fish Commission, but were not located in this survey.

PHYLUM COELENTERATA

CLASS HYDROZOA

ORDER TRACHYMEDUSAE

Family Petasidae

Gonionemus murbachii Mayer—This petasid was collected in salinities to 60‰.

CLASS SCYPHOZOA

ORDER RHIZOSTOMAE

Family Stomolophidae

Stomolophus meleagris Agassiz—The cabbage-head was common at salinities to 60‰ at all stations in April and May.

ORDER SEMAEOSTOMEAE

Family Ulmaridae

Aurelia aurita (Linnaeus)—The four-leaf clover jelly was found in salinities to 60‰.

ORDER TUBULARIAE

Family Bouganvillidae

Nemopsis bachei Agassiz—This species was present throughout the area and was of nuisance scope in April and May in salinities to 45‰. It can tolerate 75‰ salinity.

PHYLUM CTENOPHORA

ORDER CESTIDA

Family Beroidae

Beroë ovata Chamisso and Eypenhardt—This was collected in salinities to 75‰.

Mnemiopsis mccradyi—abundant.

PHYLUM PLATYHELMINTHES

Planktonic forms only were found, and are not yet identified.

PHYLUM NEMATHELMENTHES

Many unidentified planktonic forms are present.

PHYLUM TROCHELMINTHES

Brachionus plicatilis—There was only one found in October, 1954, in water of 30‰.

PHYLUM ANELLIDA

ORDER POLYCHAETA

Family Neridae

Nereis pelagica occidentalis Hartman—This polychaete was very abundant among barnacles, worm tubes, shell, and among roots of vegetation. It was eagerly sought as food by fishes. It withstood salinities to 75‰.

Family Spionidae

Polydora ligni Webster—This form apparently has the same tolerances as the above species.

PHYLUM ARTHROPODA

CLASS CRUSTACEA

ORDER COPEPODA

Acartia tonsa Dana—This was the most abundant item in almost every plankton sample. Over 7,000,000 were taken in one liter of sample. It was most abundant in October and November; numerous nauphlid forms were present at all times. They often contained reddish submicroscopic plankters in the digestive tract. It was widely utilized as food by small fish and withstood salinity of at least 80‰ but was not abundant in waters of low salinity.

Family Metidae

Metis japonica (Edwards)—This species was not as abundant as the above form but was found in every sample. One pure sample of 1,000,000 per liter was taken at the landcut in July, 1953. It tolerated extremely high salinity but it has not been found as a food item.

Family Caligidae

Caligus repax Milne Edwards—This parasite occurred at least on 35 species of fish. It was common on all Sciaenids and was found in salinities to 45‰.

C. bonito Wilson—This parasite was very common on body of redfish, drum and sea trout in waters below 45‰ salinity.

C. praetextus Bere—This species was common on menhaden in waters of low salinity, below 45‰.

Family Bomolochidae

Bomolochrus teres Wilson—The mouth and gills of menhaden harbored this parasitic copepod.

Family Pseudocynidae

Lernaeenicus longiventris Wilson—This was collected on the gular region of drum.

Lernaeenicus radiatus LeSueur—This was found on menhaden and on sawfish which served as hosts for this species.

ORDER CIRRIPEDIA

Family Balanidae

Balanus eburneus Gould—The ivory barnacle was very common and occupied the lower two-thirds of the piling habitat. It withstood high salinity but did not spawn in waters above 45‰.

Balanus amphitrite Darwin—This small purplish barnacle was found on the upper one-third of pilings and was more abundant in areas of lower salinity.

MALACOSTRACA

ORDER ISOPODA

Family Cymothainae

Nerocila acuminata Schioedte & Meinert—This isopod was collected from a filefish taken on Station 26. Isopods were rare in the hypersaline waters of the Laguna Madre. This one was in water of 45‰.

Order Amphipoda

Amphipods were found throughout the area under dead grass, among grass roots, in old worm tubes, on pilings and among barnacles. They were all readily used as food by small fish. The greatest abundance was in May and in September. They were tolerant of high salinity but were not abundant above 50‰.

Gammarus mucronatus Say—This was the most abundant of the amphipods.

Notrotropis sp.—This comprised about one percent of the total amphipod population.

Corophium louisianum Shoemaker—This species was rare in this area.

The two following amphipods were listed by Hedgpeth (1953) as occurring in Baffin Bay, and probably also occur in the upper lagoon.

Podocerus brasiliensis.

Grandidierella bonnieroides K. Stephensen

DECAPODA

Family Peneidae

Penaeus setiferus (Linnaeus)—The white shrimp was found in the Laguna Madre, but its presence was rigidly controlled by salinity and water temperature. In general, it was most abundant after heavy rainfalls. It may have remained in the area all winter in muddy regions. Usually it was restricted to the area from the Pure Oil Channel northward to the causeway. Large individuals, 150–180 mm., were found in the Intracoastal Waterway; smaller ones were found on grassy flats at salinities below 45‰.

Penaeus aztecus Ives—Brown shrimp.

Penaeus duorarum Burkenroad—Pink shrimp.

Both of these grooved, commercial shrimp were found in the upper Laguna Madre but *Penaeus aztecus* made up about 90 per cent of the population. It occupied a larger range and was tolerant of salinity to 69‰. Above 45‰ the number was sharply reduced. Most were found in the uper regions of the Intracoastal Waterway, around Pita Island, and on the flats. In the landcut in June a large population was often present; as many as 1,000 were captured in one short seine drag. The average size at that time was 80–90 mm.

Family Palaemonidae

Palaemonetes vulgaris (Say)—A few were collected in the extreme northern section.

Palaemonetes pugio Holthuis—This was located in water of low salinity near the causeway.

Palaemonetes intermedius (Holthuis).

The latter form was extremely common during all of the warmer months and lived in salinity to 60‰. It was found primarily in vegetation, living or dead. Spawning occurred in every month except January; the peak was in May.

They were commonly mistaken for young brown or white shrimp by local fishermen. The young grooved shrimp in turn were often called "grass shrimp."

Latreutes parvulus (Stimpson)—One only was found in water of 38‰.

Family Crangonidae

Crangon heterochaelis (Say)—The pistol shrimp was very rare in the area.

Family Paguridae

Pagurus sp.—The hermit crab was scarce, but strayed in occasionally from Corpus Christi Bay.

Family Xanthidae

Neopanope texana texana (Stimpson)—Mud crabs were commonly collected on old trot line stakes among barnacles. They spawned in the area and were collected in salinity as high as 60‰.

Menippe mercenaria (Say)—Stone crabs were not common in the area but could be found on occasion on the extreme nothern flats.

Family Portunidae

Callinectes sapidus Rathbun—The blue crab was abundant particularly in smaller sizes until the salinity reached 45‰. A few were found in water of 60‰. The shallow grassy flats contained many small "dugouts" each housing a crab. The spawning cycle was definitely different from that of other bays. "Sponge crabs" (egg-bearing females) were numerous in January and February provided the salinity was not above 45‰.

Callinectes danae Smith—The Gulf crab was similar in its range, habits, and tolerance to the blue crabs, but was the more abundant of the two at salinities above 45‰.

Family Ocypodidae

Uca pugilator (Bosc)—The fiddler crab was in evidence all along the shoreline.

PHYLUM MOLLUSCA

CLASS PELECYPODA

ORDER EULAMELLIBRANCHIA

Family Mactridae

Mulinia lateralis Say—This bivalve had ben reported as being extremely abundant in the upper Laguna Madre but investigation revealed that is comprised less than ten percent of the total live shell present. Scattered individuals were collected from the causeway to South Bird Island. In 1956 many specimens were obtained from deep mud in the lower areas at salinities near 45‰. Some appeared to be two years old but certainly not older. It is probably not tolerant of salinity above 45‰ when combined with high temperature.

Veneridae

Anomalocardia cuneimeris Conrad—This, the most abundant mollusk in the Laguna Madre, was very tolerant of high salinities. The primary food item of the black drum, this small bivalve was found buried just below the surface and on the surface. It was found closely associated with shoalgrass. Hedgpeth (1953) calculated length frequencies on the species for Baffin Bay in May, 1951. Work of a similar nature was done in July, 1955 near Pita Island. The results were as follows:

Length mm.	Number of Individuals	
	Baffin Bay	Pita Island
2	0	3
3	4	13
4	11	50
5	13	50
6	27	98
7	(80)	301
8	57	(532)
9	53	(591)
10	17	76
11	9	54
12	4	12
13	1	12
14	0	56
15	0	(80)
16	0	(96)
17	0	8
18	0	4
Total	276	2,036

These data for Pita Island indicate two year classes in the area, that is, the 8-9 mm. and 15-16 mm. sizes.

Family Corbiculidae

Pseudocyrena floridana Conrad—A few live individuals were collected near North Bird Island and on Station 25. Many recently dead shells were found intact on the spoil banks near Bird Island.

Family Tellinidae

Tellina tampaensis Conrad—These were collected near North Bird Island throughout 1955. Mortality was heavy probably due to excessive salinity.

Macoma brevifrons (Say)—R. H. Parker of the Scripps Institute of Oceanography, University of California in a personal communication, stated that he found this species alive on one occasion in the upper lagoon and that fresh dead shell was abundant.

ORDER MEGAGASTROPODA

Family Cerithiidae

Bittium varium (Pfeiffer)—This species was located among vegetation near station 25A and was identified by R. H. Parker.

ORDER TECTIBRANCHIA

Family Pyramidellidae

Odostomia bisuturalis Say—R. H. Parker, in a personal communication, stated that he found many individuals either alive or dead in the region under study.

Further information on the macro-vertebrates of the Texas coast is given by Parker (1955), (1956). Some of this information may be applicable to the upper Laguna Madre.

PHYLUM CHORDATA (Vertebrates)
CLASS PISCES

SUBCLASS ELASMOBRANCHII

ORDER EUSELACHII

Family Carcharhinidae

Aprionodon isodon (Müller and Henle)—Only one smooth-tooth shark was taken in April, 1954.

Carcharhinus limbatus (Müller and Henle)—The black-tipped shark was occasionally plentiful during less saline periods.

ORDER BATOIDEI

Family Pristidae

Pristis pectinatus Latham—Two sawfish were taken in the area but they apparently were not tolerant of high salinity.

Family Dasyatidae

Dasyatis americana Hildebrand and Schroeder—A few southern sting rays were found near the causeway but they were not tolerant of high salinity.

Dasyatis sabina (Le Sueur)—The stingaree was more common than the sting ray but did not withstand salinity above 45‰.

Family Rhinoperidae

Rhinoptera bonasus (Mitchill)—Very large cow-nosed rays were abundant during springs months if the water temperature was below 25° C. and salinity below 60‰. Combination of high salinity and temperature sharply reduced the number. They were captured at every station. Young were produced in the area.

ORDER HOLOSTEI

Family Lepisosteidae

Lepisosteus spatula (Lacépède)—The alligator gar was never common in the area but was collected near the causeway in water of low salinity.

ORDER NEMAGOGNATHI

Family Ariidae

Bagre marina (Mitchill)—The gafftopsail catfish was not present at salinities above 45‰.

Galeichthys felis (Linnaeus)—The sea catfish was very common to 45‰ salinity, limited sharply at 60‰, and absent above this point.

ORDER APODES

Family Ophichthidae

Ophichthus sp.—Two only were taken in a salinity of 37‰.

Family Anguillidae

Anguilla rostrata (Le Sueur)—Only one was taken in a salinity of 38‰ at marker 39.

ORDER ISOPONDYLI

Family Elopidae

Elops saurus Linnaeus—The tenpounder or skipjack was very common in the Laguna Madre. It apparently spawned there and tolerated water of any salinity recorded in this survey. Young were present in the Point of Rocks area in December and January and throughout the area in the summer months. It was consumed readily by large trout.

Family Megalopidae

Tarpon atlanticus (Valenciennes)—The tarpon was definitely a stray in the area; only six were taken.

Family Clupeidae

Harengula pensacolae Goode and Bean—This species was found in the landcut in July, 1954, 1955, and 1956.

Opisthonema oglinum (Le Sueur)—The threadfin herring was rare, about 12 were taken during the survey.

Brevoortia gunteri (Hildebrand)

Brevoortia patronus Goode—Menhaden, particularly *Brevoortia gunteri*, were very common in waters of moderate salinity, and present in water of high salinity. They definitely spawned in the area in February, 1956. Individuals from 15 mm. up were taken in March, April, and May.

Dorosoma cepedianum (Le Sueur)—The gizzard shad was very abundant at station 32 in April, 1956 in salinity of 37.5‰. All were moving southward.

Family Engraulidae

Anchoa hepsetus (Linnaeus)—This anchovy was very common around islands and spoil banks and in sheltered coves. It preferred sandy bottom and was one of the most abundant fishes of the area. It withstood salinities of 75–80‰, but preferred salinity below 50‰. It moved ahead of the more saline water. The anchovy was not noted as a food item for other fishes.

Anchoa mitchilli—like the above species.

ORDER INIOMI

Family Synodontidae

Synodus foetens (Linnaeus)—The lizard fish was not present in salinities above 40‰ except in the landcut where many were taken in June and July, 1954, 1955 in salinities up to 60‰.

ORDER HAPLOMI

Family Cyprinodontidae

Fundulus similis (Baird and Girard)—This killifish, called "chub" locally, was present during all seasons and was euryhaline. It was the second most abundant cyprinodont of the area. It spawned during warmer months in vegetation.

Fundulus pulvereus

Several individuals closely resembling *Fundulus similis* have been taken.

Fundulus grandis Baird and Girard—This large species was abundant in sheltered areas in salinities of 30–45‰. It spawned in the areas of dead vegetation.

Cyprinodon variegatus Lacépède—The broad killifish was very common in waters from 5 to 75‰ at all temperatures. It was a common food item and was called "black chub" locally.

ORDER SYNENTOGNATHI

Family Belonidae

Strongylura marina (Walbaum)—Billfish were present during warmer months particularly in the landcut. They were not common in the bay area proper at salinities above 45‰ but in this one location were in water of 55–60‰ salinity. They were gravid in July.

Family Hemiramphidae

Hyporhamphus unifasciatus (Ranzani)—The halfbeak was not common in the area.

ORDER LOPHOBRANCHII

Family Syngnathidae

Syngnathus louisianae (Günther)

Syngnathus scovelli (Evermann and Kendall)—These two pipefish were abundant is vegetation in salinities up to 45‰. They both spawned in the area in May and June, 1956.

ORDER ACANTHOPTERI

SUBORDER PERCESOCES

Family Atherinidae

Menidia beryllina peninsulae (Goode and Bean)—Tidewater silversides were extremely abundant to 45‰ salinity They tolerated a range from 10 to 75‰ regardless of water temperature. Gravid females were obtained in any month on any station. This was a very common food item for larger fish. A total length of 125 mm. was not uncommon.

Family Mugilidae

Mugil cephalus Linnaeus—The striped mullet was very common throughout the area all year. It was euryhaline. It spawned in the area in December in waters below 45‰. It was occasionally taken very large, up to seven pounds.

Mugil curema Valenciennes.—The white mullet was common but not abundant. None were taken in water above 50‰.

SUBORDER SCOMBROIDEA

Family Scombridae

Scomberomorus maculatus (Mitchill)—The Spanish mackeral was a straggler in the area.

Family Carangidae

Caranx hippos (Linnaeus)—The common jackfish was common in the landcut in warmer months and was scattered throughout the bay at this time. It tolerated salinities up to 60‰. Individuals ranged in size from 45 mm. to 500 mm.

Vomer setapinnis (Mitchill)—Moonfish.

Chloroscombrus chrysurus (Linnaeus)—Bumper.

Selene vomer (Linnaeus)—Lookdown. This and the two preceding carangids were common in salinities to 40‰ from October through December.

Trachinotus carolinus (Linnaeus)—Very large schools of common pompano were present throughout the area in September and October in salinities of 45-50‰.

Family Pomatomidae

Pomatomus saltatrix (Linnaeus)—The bluefish was a stray in salinities of 35‰ or less.

Family Stromateidae

Peprilus paru (Linnaeus)—Harvest fish.

Poronotus triacanthus (Peck)—Butter fish. Both stromatoids were present on all stations in September, October, November, and December, provided salinity was not much above 40‰.

SUBORDER PERCOIDEA

Family Lobotidae

Lobotes surinamensis (Bloch)—The tripletail was found only in the landcut.

Family Haemulidae

Orthopristis chrysopterus (Linnaeus)—Pigfish were common on the flats in April and May and in the landcut throughout the year. Individuals of 30-35 mm. standard length were taken at Pita Island in May, 1954 at a salinity of 43‰. Individuals in the landcut ranged in size to 490 mm. and were in water of 56‰ salinity.

Family Sparidae

Lagodon rhomboides (Linnaeus)—Pinfish were very common through the area in summer months at all recorded salinities. They were present in winter but were not abundant. They died quickly when trapped in hypersaline waters. Young (10-25 mm.) specimens were taken in plankton tows in March, 1955. No ova were found but may have been present. This species was found to be a very valuable forage fish and much used by commercial fishermen as bait for large trout. Individuals were recorded up to 437 mm. total length in the landcut.

Archosargus probatocephalus (Walbaum)—Sheepshead were fairly common, particularly from December through March, in salinities of 40‰ or less. The few present at higher salinities were probably strays. They spawned in February and March but not in this area.

Family Gerridae

Xystaema cinerum (Walbaum)—The gray moharra was common whenever salinity was 40‰ or less.

Family Sciaenidae

Cynoscion arenarius Ginsburg—Sand trout were not especially common but were found in the Intracoastal Waterway, particularly in December and January. They were less plentiful in salinities above 45‰.

Cynoscion nebulosus (Cuvier)—Spotted Sea Trout. Any calculation of the distribution of weakfish or "trout" should consider at least two size ranges. Some larger trout, above four pounds, appeared never to leave the upper Laguna Madre. These were found, in limited numbers, throughout the year despite changes in salinity from 25‰ to 75‰ and in temperature from 4° to 33° C. The area known as "Point of Rocks" was noted as their habitat. Some of these moved northward out of the upper Laguna Madre in the spring and summer, and many were present in the landcut at this time.

Smaller trout were more sensitive to hypersalinity but were usually present in the area in all months, although combinations of high salinity and high temperature limited the number severely. They were most abundant in April and May and in October. Many were present in the deep water of the landcut in June, July, and August. They did not spawn in waters above 45‰ and were very sensitive to crowding from other fish, particularly black drum. Populations in the landcut in the summer normally moved southward.

Trout greater than 500 mm. total length were piscivorous in the upper Laguna Madre. Examination was made of 200 stomachs which contained food. Twelve had consumed ten-pounders, six had eaten small trout, and 182 had consumed mullet. On several occasions mullet 14 inches long were found partially ingested by trout only 21 inches long. A preferred food item in the landcut during May, June, and July, 1955 and 1956 was *Cyprinodon variegatus.*

More large trout were found in the upper Laguna Madre than in the Aransas Bay area (Figure 10). Trout of eight to nine pounds were abundant and individuals of

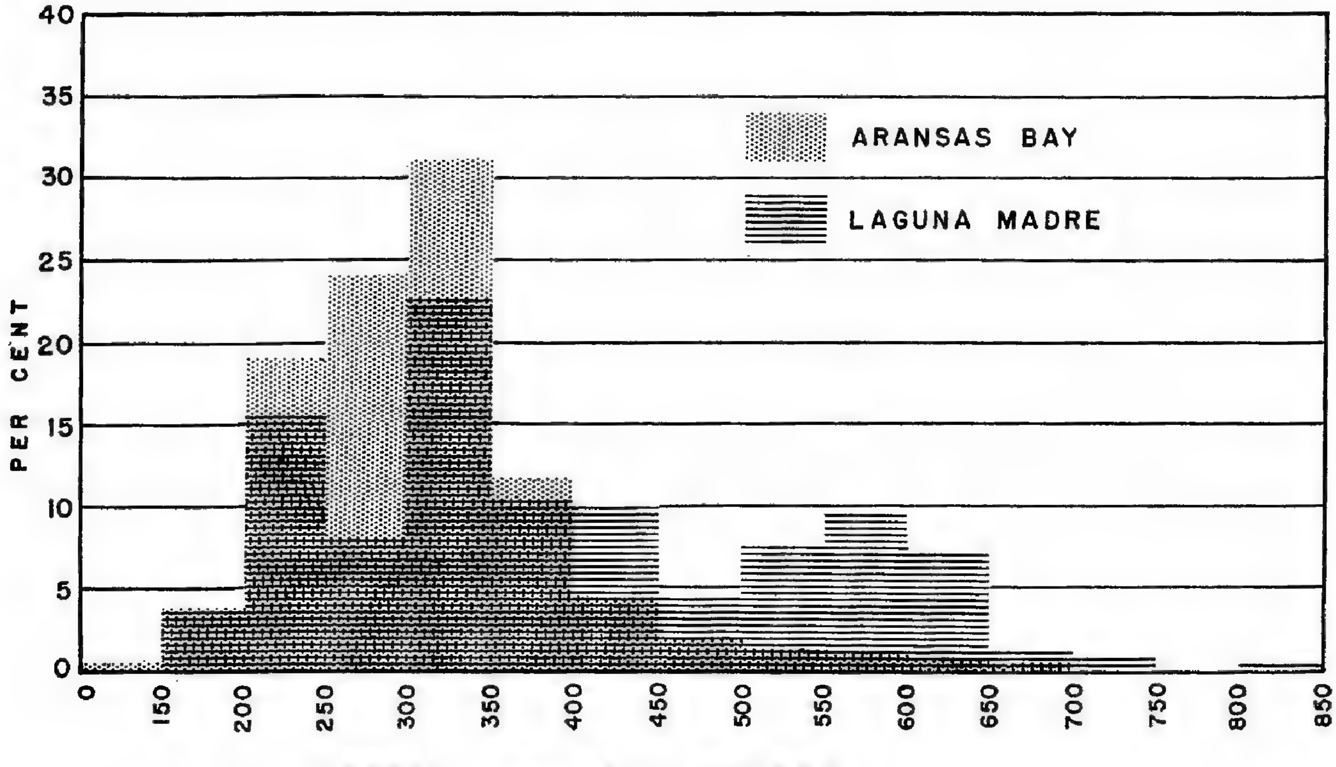

Fig. 10. Percentage composition according to size of *Cynoscion nebulosus* taken in Laguna Madre and in Aransas Bay.

twelve pounds were not rare. Three individuals which weighed 15 pounds each were collected at Station 37 in March, 1952.

Sciaenops ocellata (Linnaeus)—Channel bass or redfish of all sizes were sensitive to high salinities combined with high temperature, but distribution was also regulated somewhat by size. In April and May large numbers of redfish five to nine inches long were present in the upper area, provided salinity was not above 45‰. These tended to inhabit secluded waters. Most of these fish left the area in June or July apparently because of competition for space. Larger redfish, ranging in size from 21 to 31 inches were present in September, October, November, December, January, and February. These probably left the area at times during the winter but returned within a few weeks. Very large redfish (up to 40 pounds) were present in the area in September and October but soon migrated. Populations were severely limited by salinity of 50‰ or above.

Redfish fed heavily on mullet and blue crabs while in the area and broad killifish were also found in the digestive tract.

Pogonias cromis (Linnaeus)—Black drum were extremely plentiful throughout the area at all times and were even more numerous from September until April. During this period they comprised over 90 percent of the sciaenid population over 12 inches long. They were not affected by salinity except as it affected food supply and spawning. This fish spawned in the area, as well as in other bays and in the Gulf, provided salinity was below 45‰. The peak of spawning was in February and March.

Over 90 percent of the food of the black drum was bivalves, alive or dead. When live shellfish were not available, dead shell was consumed.

It appears that black drum grow to 225 mm. in one year, to 285 mm. in two years, and approximately 50 mm. per year thereafter.

Bairdiella chrysura (Lacépède)—Silver perch were present only in salinity of 45‰ or less.

Leiostomus xanthurus (Laépède)—The spot was apparently tolerant of high salinity but was more abundant in areas below 50‰. It did not spawn in area but was usually present from 25 mm. to above 200 mm. with the young appearing in December.

Micropogon undulatus (Linnaeus)—Croakers were present throughout the area and tolerated hypersalinity to 70‰. Smaller individuals were very numerous but this fish probably did not spawn in the area.

Menticirrhus littoralis (Holbrook)—Southern kingfish were never abundant but were present in salinities of 45‰.

Family Balistidae

Balistes carolinensis (Gmelin)—The triggerfish was a stray in the area.

Family Monacanthidae

Alutera schoepfi (Walbaum)—Orange filefish were observed in pairs in September and October, 1955, in water of 30‰ and were occasionally taken in salinities to 50‰ over grassy flats.

SUBORDER GYMNODONTES

Family Tetraodontidae

Sphoeroides nephelus (Goode and Bean)—Swellfish were fairly common in warmer months around Pita Island and the upper spoil banks.

SUBORDER CRANIOMI

Family Scorpaenidae

Scorpaena plumieri Bloch—The scorpionfish spawned near Station 26 in May in salinity of 38‰.

Family Triglidae

Prionotus martis Ginsburg—The sea robins were common on upper stations in salinities to 45‰.

Prionotus scitulus latifrons Ginsburg.

Prionotus tribulus crassiceps Ginsburg.

SUBORDER GOBIOIDEA

Family Gobiidae

Gobiosoma bosci (Lacépède)—This goby was very abundant throughout the year in water up to 45‰ salinity. It lived and spawned in vegetated areas.

Gobionellus oceanicus (Pallas)—This goby was found only on the upper flats, in April, 1956.

SUBORDER TRACHINOIDEA

Family Uranoscopidea

Astroscopus y-graecum (Cuvier and Valenciennes)—The southern star-gazer was rare in the area if the salinity was above 30‰.

SUBORDER HAPLODOCIA

Family Batrachoididae

Opsanus beta Goode and Bean—Toadfish were very common in warmer months around pilings and in channels in salinities up to 45‰.

SUBORDER OPHIDIODEA

Family Gadidae

Urophycis floridanus (Bean and Dresel)—Florida ling were seldom found in water above 30‰.

SUBORDER HETEROSOMATA

Family Bothidae

Paralichthys lethostigma Jordan and Gilbert

Paralichthys albigutta Jordan and Gilbert—Both species of *Paralichthys* were fairly common throughout the area but were sharply limited by salinity above 45‰ except in the landcut. They were occasionally found at salinities of 60‰.

Ancylopsetta quadrocellata Gill—This fluke was not common but was found in water with salinity below 45‰, usually in channels.

Citharichthys spilopterus Günther—This form was abundant at salinities below 60‰ in the landcut and around Pita Island.

Etropus crossotus Jordan and Gilbert—The fringed flounder was rather rare, being found in the fall in water of 45‰ or less.

Family Achiridae

Trinectes maculatus fasciatus (Lacépède)—The hogchoker was common in fall months in water of 50‰ or less.

Family Cynoglossidae

Symphurus plagiusa (Linnaeus)—The tonguefish was rare; it did not tolerate salinity much above 35‰.

Interrelationships

HYDROGRAPHICAL AND METEOROLOGICAL

The most evident relationship in the upper Laguna Madre was that between autumn rainfall and salinity the year following. Fainfall during spring months normally produced little runoff and seldom affected salinity appreciably. Average summer temperature varied little from year to year (Table 2). Humidity was relatively constant; therefore total evaporation may have varied little from year to year. These factors were constant but rainfall was not. Heavy autumn rainfall resulted in relatively low salinity the following year. By estimating the future salinity it was possible to get a fairly accurate preview of conditions in the upper Laguna Madre the following year.

Certain organisms were prevalent only at or below set salinity levels. The most notable of these levels were at 45‰ and 60‰. Therefore, the effect of rainfall could be evaluated by using these criteria.

TABLE. 6

Correlation of Rainfall and Salinity

					Average Salinity	
Year	Rainfall Previous Autumn (Rain (inches) Sept., Oct., Nov.	Rainfall Rest of Year	Total Year	Days Below 45 o/oo	Days Above 45 o/oo	Days Above 60 o/oo
1952	17.0	12.0	29.0	206	140	20
1953	8.5	3.25	11.75	3	270	92
1954	20.5	7.5	28.0	125	240	0
1955	8.75	5.0	13.75	65	230	70

It was apparent that the amount of autumn rainfall regulated salinity in that the days of salinity above 60‰ varied almost directly with the number of inches of rainfall.

TIDAL EFFECTS ON SALINITY

Hedgpeth (1946) recorded a complete overturn of waters in the upper Laguna Madre during the fall equinoctial tide; the tide decreased salinity progressively southward with each rise at Corpus Christi Bay. Several weeks were required for tidal effects to be felt throughout the area, and it is probable that wind action on the saline blocks in

Baffin Bay and the area south of that bay affected these figures somewhat.

This turnover did not occur during the survey. Possibly this was due to the restriction of waterflow caused by the landfill causeway at the northern end of the lagoon. At any rate, the section between Station 30 and Station 34 was virtually unaffected by tidal action (Table 7).

Prior to dredging of the Intracoastal Waterway fresher water from Corpus Christi Bay moved in a thin layer over the entire lagoon with mixing only at the extreme northern end (Figure 11). During this survey a certain amount of layering occurred between Markers 63 and 75 but the entire northern flat was devoid of lagoon water and

TABLE 7

Comparison of Effects on Salinity of Autumn High Tides Before and After Dredging of the Intracoastal Waterway

	Hedgpeth (1946) Salinities								Simmons (1954) Salinities				
Location	July 25	Aug. 3	Aug. 10	Aug. 17	Aug. 22	Aug. 29	Sept. 16	Sept. 14	Aug. 12	Aug. 23	Sept. 14	Sept. 27	Oct. 25
Pita Island	40.0	36.6	41.3	35.3	35.6	37.2	35.9	35.1	49.5	54.7	45.0	45.5	53.0
Station 27	------	------	------	------	------	------	------	------	48.6	46.6	45.0	45.5	54.0
South Bird Island	75.4	54.4	64.6	36.9	40.6	37.2	42.1	37.3	------	------	------	------	------
Griffen	------	------	------	------	------	------	------	------	51.0	52.6	48.6	45.0	51.0
Point of Rocks	78.7	80.0	78.0	64.6	52.7	81.0	50.7	70.8	46.5	52.0	54.0	52.0	51.3
Penascal Point	99.2	102.7	101.2	94.0	90.4	91.4	90.5	80.6	46.8	50.0	56.0	56.0	49.8
Landcut	------	------	------	------	------	------	------	------	46.5	48.4	54.8	52.0	44.6

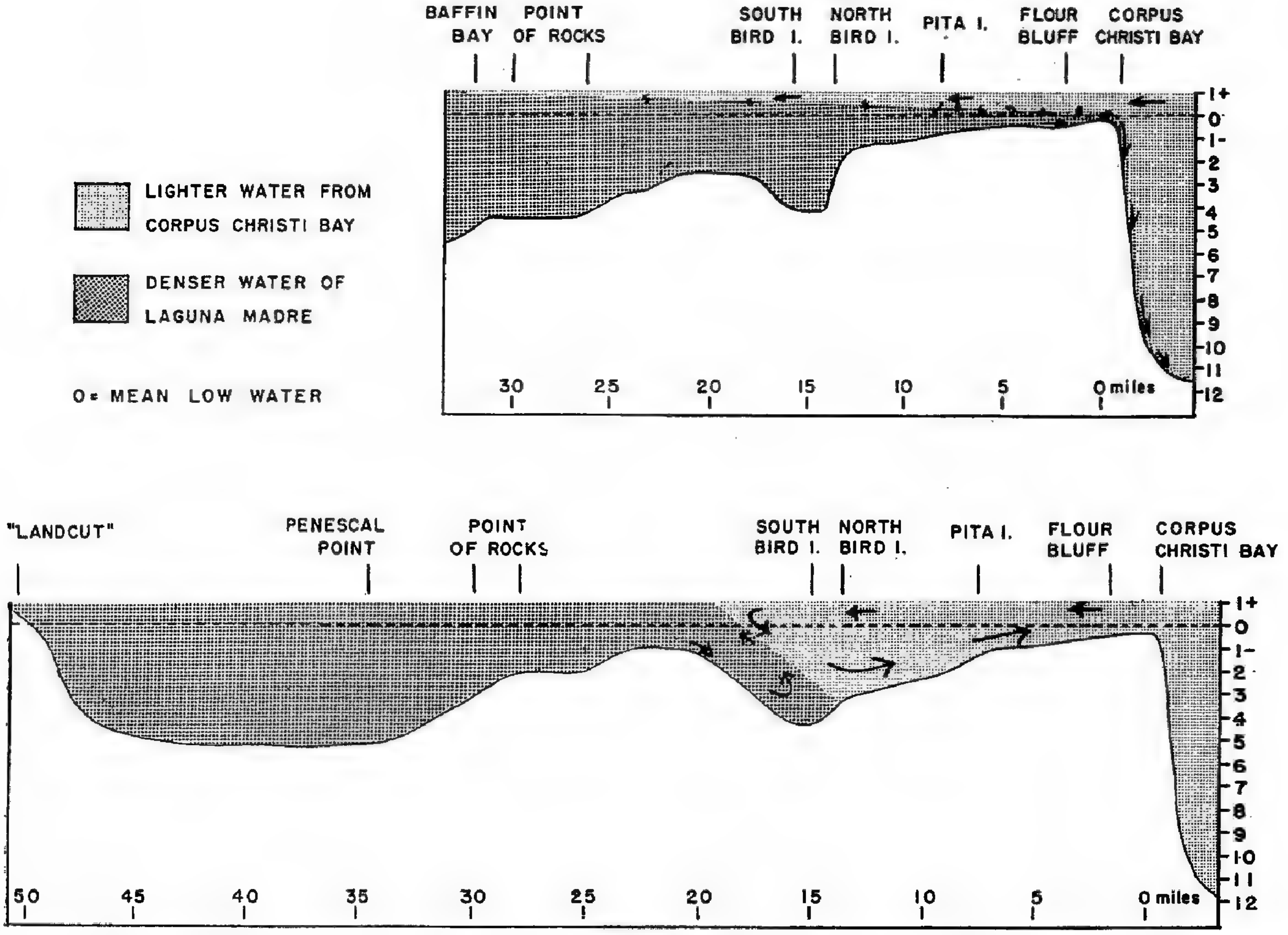
BAFFIN BAY
POINT OF ROCKS
SOUTH BIRD I.
NORTH BIRD I.
PITA I.
FLOUR BLUFF
CORPUS CHRISTI BAY
LIGHTER WATER FROM CORPUS CHRISTI BAY
DENSER WATER OF LAGUNA MADRE
0 = MEAN LOW WATER
1+ 0 1- 2 3 4 5 6 7 8 9 10 11 12
30 25 20 15 10 5 0 miles
"LANDCUT"
PENESCAL POINT
POINT OF ROCKS
SOUTH BIRD I.
NORTH BIRD I.
PITA I.
FLOUR BLUFF
CORPUS CHRISTI BAY
1+ 0 1- 2 3 4 5 6 7 8 9 10 11 12
50 45 40 35 30 25 20 15 10 5 0 miles

FIG. 11. Schematic profiles of salinity conditions in Laguna Madre at one foot tide. Above: after Hedgpeth, 1946. Below: Simmons, 1955.

the sector south of Marker was devoid of the fresher Corpus Christi Bay water (Figure 11). This was caused by water piling up on the southern end and by turning under of water in the Intracoastal Waterway at this critical point. Actually, an incoming tide of 1.0 foot resulted in 1.5 foot tide at the landcut provided the wind was with the tide. With a wind against the tide this stacking up of water was neutralized. Tidal effect thus was temporary as fresher water tended to withdraw into Corpus Christi Bay during low tide.

SALINITY AND TEMPERATURE

Correlation between salinity and temperature was noteworthy only in relation to evaporation. Evaporation was greater during hot, dry days, and the salinity increased at these times. A strong correlation existed between salinity and temperature and the biota. In general, high temperatures coincided with high salinity. However, when autumn rainfall was light, high salinity sometimes concurred with low temperature. For example, a salinity of 60.9‰ and a water temperature of 12.0° C. was recorded in December, 1954.

SALINITY, TEMPERATURE, AND FAUNA

When high salinity and low temperature coincided, many forms not normally tolerant of hypersalinity were present. Some of these were blue crabs, amphipods, flounder and redfish. In a similar fashion many forms such as the bivalves tolerated extremely high water temperature provided salinity was low. Thus, it may be stated that high salinity and high temperature combine to limit the number of species. The number of species present was found to vary according to two different temperatures and two very similar sets of salinities (Figure 12).

SALINITY AND FAUNA

Considering the normal phases of salinity and temperature, certain facts stood out concerning salinity and fauna. The higher the salinity:

1. The fewer the species. 2. The greater the number of individuals of each species available. 3. The larger the average individual of each vertebrate species. 4. The smaller the average individual of many invertebrate species—i.e. blue crabs, barnacles.

Water with salinity of 40–50‰ appeared to be optimum for many forms and water above or below this eliminated or reduced in number many species. A total of 51 identified species lived within this range as compared with 21 species which lived only below this range and 40 species which lived above it.

Only two forms, both planktonic, were reduced in number as the salinity was decreased to 45‰, but at least 20 forms were reduced in number after salinity fell below 40‰.

Many species were actually more abundant at moderately high salinity. A noteworthy species was the bivalve *Anomolocardia cuneimeris*. One large bed near Pita

TABLE 8

Species normally collected at salinities from 25‰ to 75‰

Nemopsis bachei
Beroe ovata
Nereis pelagica occidentalis
Polydora ligni
Acartia tonsa
Metis sp.
Balanus eburneus
Balanus amphitrite
Gammarus mucronatus
Nototropis sp.
Corophium louisianum
Anomolocardia cuneimeris
Elops saurus
Anchoa hepsetus
Fundulus similis
Cyprinodon variegatus
Menidia beryllina peninsulae
Mugil cephalus
Lagodon rhomboides
Cynoscion nebulosus
Pogonias cromis
Micropogon undulatus

Species normally collected at salinities from 20‰ to 60‰, but rarely above 60‰

Stomolophus meleagris
Gonionemus murbachi
Penaeus aztecus
Penaeus duorarum
Palaemonetes intermedius
Neopanope texana texana
Callinectes sapidus
Callinectes danae
Galeichthys felis
Brevoortia gunteri
Brevoortia patronus
Caranx hippos
Orthopristis chrysopterus
Cynoscion nebulosus—small individuals
Leiostomus xanthurus
Paralichthys lethostigma
Paralichthys albigutta
Citharichthys spilopterus

Species collected at salinities from 25‰ to 45‰, but not common above 45‰

Ceratium tripos
Ceratium fusus
Aurelia aurita
Caligus rapax
Caligus bonito
Caligus praetextus
Bomolochrus teres
Lernaeenious longiventris
Lernaeenious radiatus
Metrocila acuminata
Penaeus setiferus
Palaemonetes vulgaris
Palaemonetes pugio
Latreutes paryulus
Uca pugilator
Mulinia lateralis
Pseudocyrena floridana
Tellina tampaensis
Dasyatis americana
Dasyatis sabina
Rhinoptera bonasus
Bagre marina
Harengula pensacolae
Synodus foetens
Fundulus grandis
Strongylura marina
Hyporhamphus unifasciatus
Syngnathus louisianae
Syngnathus scovelli
Vomer setapinnis
Chloroscombrus chrysurus
Selene vomer
Trachinotus carolinus
Peprilus paru
Poronotus triacanthus
Lobotes surinamensis
Mugil curema
Archosargus probatocephalus
Xystaema cinereus
Cynoscion arenarius
Bairdella chrysura
Menticirrhus littoralis
Alutera schoephi
Spheroides nephelus
Prionotus martis
Prionotus tribulus crassiceps
Gobiosoma bosci
Opsanus beta
Ancylopsetta quadrocellata
Etropus crossotus
Trinectes maculatus fasciatus

The following species were common from 25‰ to 35‰ but were rarely collected above 35‰

Bachionus plicatilis
Crangon heterochaelis
Pagurus sp.
Menippe mercenaria
Aprionodon isodon
Carcharhinus limbatus
Anguilla rostrata
Pristis pectinatus
Lepisosteus spatula
Tarpon atlanticus
Opisthonema oglinum
Dorosoma cepedianum
Ophichthus ocellatus
Scomberomorus maculatus
Pomatomus saltatrix
Balistes carolinensis
Scorpaena plumeri
Astroscopus y-graecum
Gobionellus oceanicus
Urophycis floridanus
Symphurus plagiusa

Island was fenced off with ¼″ hardware cloth and with cheesecloth and was checked over a period of four years. The relationship to salinity was as follows:

Salinity (o/oo)	Average Number of Live Bivalves Per Square Foot
25	125
35	400
45	1400
60	440
79	000 (W.T. 33.0)
60	400 (new plot)
45	1200
25	10

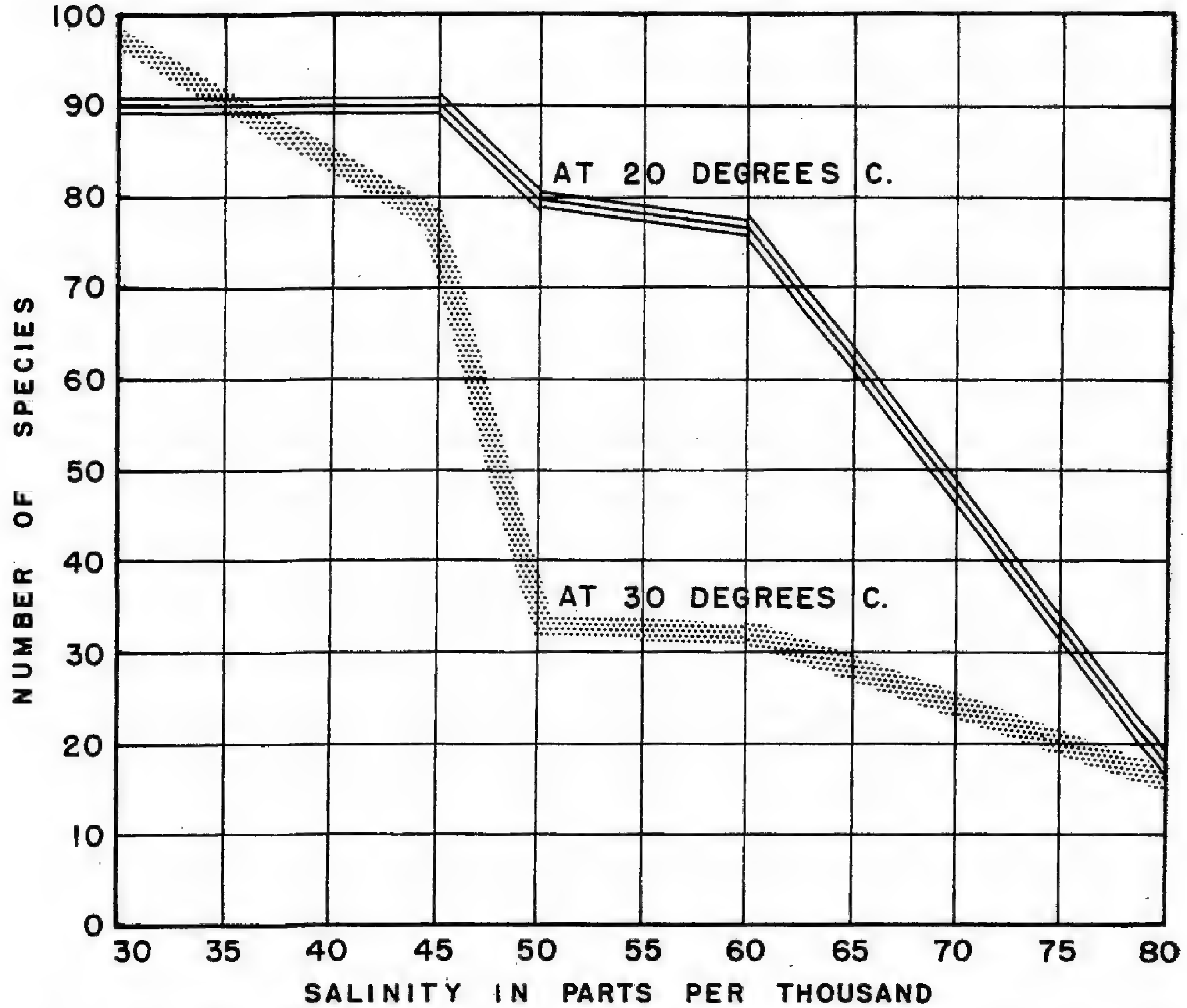

Fig. 12. Abundance of animal species relative to salinity and temperature in upper Lagunda Madre.

Shells were screened with graduated mesh pans so that all sizes were obtained. Spawning apparently was regulated by salinity and temperature rather than by season. The distribution also of this same species was governed by salinity although high water temperature eliminated shallow water beds.

Redfish of the 0 year class reacted to salinity of 54‰ or less by utilizing the upper lagoon as a nursery in spring months. If the salinity was above this point, they did not enter the area. Young trout and penaeid shrimp reacted in similar fashion.

Most species withstood rising salinity if they were present before the rise occurred. Many present at 35‰ remained until a 60‰ level was reached whereas they did not enter directly from 35‰ water to water of 60‰. It appears that within limits, the rapidity of salinity change is of more importance than the actual salinity.

RELATIONSHIP OF SALINITY TO VEGETATION

Three species of plants were common in the area. In 1956 several species of algae were abundant at salinities of 30–38‰ but these soon vanished. All vegetation distribution varied in distribution under optimum and adverse conditions (Figure 13).

RELATIONSHIP OF FLORA TO FAUNA

Angiosperm vegetation was of primary importance to the fauna of this area. Vegetated areas served as spawning grounds for several species such as trout and gobies and certain species did not inhabit an area unless vegetation was present. Somes forms which lived primarily among "grass" are: polychaets, amphipods, penaeid shrimp (young), palaemonid shimp, pistol shrimp, crabs, bivalves, mollusks, killifish, pipefish, gobies, and toadfish. Pinfish and pigfish preferred areas near vegetation or rocks. Many species of migratory waterfowl winter in the area and feed on shoalgrass.

Certain forms spawned only in vegetation. The spotted trout preferred *Ruppi maritima* but would utilize *Diplanthera wrightii.* All of the previous species listed except penaeid shrimps, crabs, pinfish, and pigfish spawned in "grass." The spawning area of the latter two forms is not known but may be in vegetation. Several fish feed on vegetation and the invertebrates thereon. Pinfish and sheepshead feed heavily on vegetation and black drum feed on bivalves and worms under the roots.

The only marine animal of the area actually harmful to vegetation was the black drum. Large schools of these fish sometimes rooted up acres of vegetation during a night of feeding.

MAN, FLORA AND FAUNA

Activities of mankind seldom lead to stability in the work of nature. Probably the largest change wrought by man in the area was the building of the earth-fill causeway and canals. Core samples taken by the writer indicated that the flats south of the causeway to Padre Island were filling in at the rate of one inch per year. In addition to taking cores, the investigator placed marked stakes in the bottom near the causeway and measured deposition in this manner. Silt, carried by the water, banked against this fill and was dumped on calm days. The restricted Intracoastal Canal dropped its silt after it passed the causeway much as a river drops silt at the mouth. Several fairly deep spots have silted up 12 inches or more. Openings between spoil banks have been reduced by fifty per cent. Oil dredging and drilling apparently silted 24 square miles near Yarborough Pass and five square miles near the Pure Oil Channel.

Pollution was regarded as nil in the area, since there is no industry except oil.

Netting was illegal in the lagoon, but it existed. Certain forms of netting were harmful. Drag seines caught fish of all sizes and destroyed spawning areas. Very small-mesh gill nets virtually destroyed some populations of small trout. Large-mesh gill nets, however, caught mostly black drum, a fish harmful to rooted vegetation. The actual catch of game and food fish by gill nets of various sizes is illustrated in Table 9.

Rod and reel fishermen were selective and tended to take only trout and redfish. Probably not enough were caught by sportsmen to affect the population.

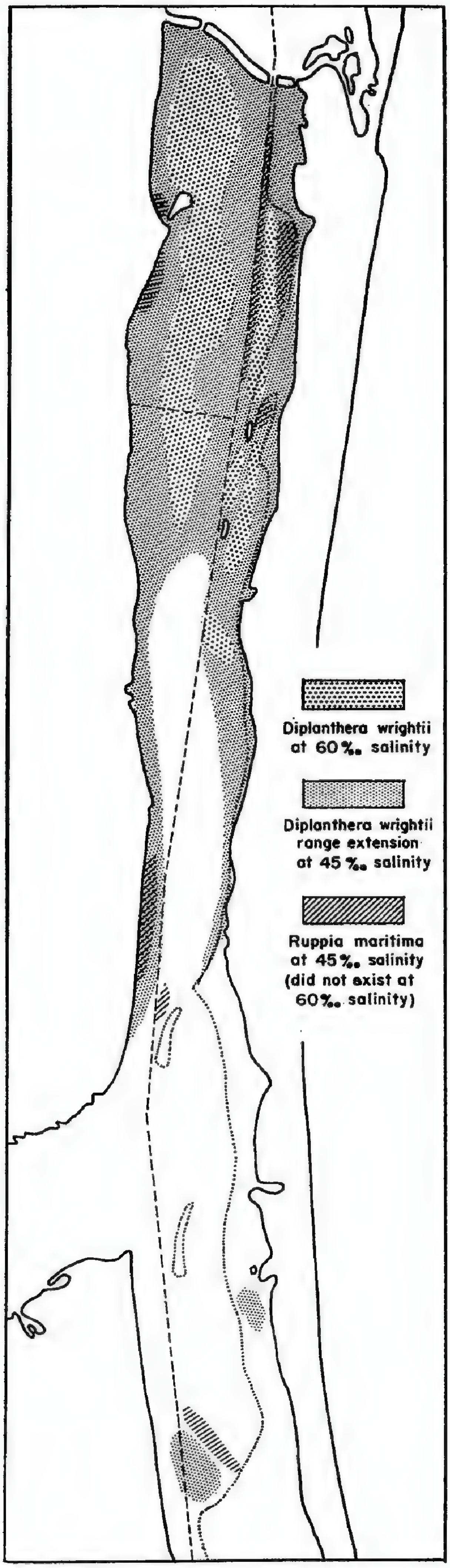
Diplanthera wrightii at 60‰ salinity
Diplanthera wrightii range extension at 45‰ salinity
Ruppia maritima at 45‰ salinity (did not exist at 60‰ salinity)

FIG. 13. Range of vegetation in upper Laguna Madre.

TABLE 9

Catch of Food and Games Fishes with Various Commercial Type Nets

Year of 1953			
January			
5″ Net	Drum	952	95.2%
	Red	22	2.2
	Trout	8	.8
	Flounder	10	1.0
	Sheepshead	6	.6
	Total	998	
February			
5″ Net	Drum	122	96.83
	Red	1	.79
	Trout	3	2.38
	Total	126	
May			
	Drum	146	91.82
	Redfish	3	1.89
	Trout	7	4.40
	Flounder	1	.63
	Sheepshead	2	1.26
	Total	159	
May			
3″ Net	Drum	584	93.75
	Red	13	2.09
	Trout	26	4.17
	Total	623	
June			
Mixed size Nets	Drum	201	84.10
	Redfish	3	1.26
	Trout	32	13.39
	Sheepshead	3	1.26
	Total	239	
July and August			
Used rods and reels instead of nets			
September			
5″ Net	Drum	58	82.86
	Redfish	2	2.86
	Trout	6	8.57
	Sheepshead	4	5.71
	Total	70	
September			
3″ Net	Drum	101	74.81
	Redfish	9	6.67
	Trout	25	18.52
	Total	135	
October			
3″ Net	Drum	176	96.70
	Trout	6	3.30
	Total	182	
November			
5″ Net	Drum	228	82.61
	Redfish	16	5.80
	Trout	11	3.99
	Sheepshead	17	6.15
	Flounder	4	1.45
	Total	276	
November			
3″ Net	Drum	148	84.09
	Redfish	14	7.95
	Trout	12	6.82
	Sheepshead	2	1.14
	Total	176	

TABLE 9—Continued

Catch of Food and Games Fishes with Various Commercial Type Nets

Year of 1954

January 5″ Net	Drum	118	80.27	
	Redfish	22	14.97	
	Trout	2	1.36	
	Flounder	4	2.72	
	Sheepshead	1	.68	
	Total	147		
January 3″ Net	Drum	215	88.11	
	Redfish	23	9.45	
	Trout	5	2.05	
	Flounder	0	....	
	Sheepshead	1	.41	
	Total	244		
February 5″ Net	Drum	36	....	
	Redfish	4	....	
	Trout	5	....	
	Flounder	1	....	
	Sheepshead	1	....	
	Total	47		
February 3″ Net	Drum	927	93.54	
	Redfish	10	1.00	
	Trout	54	5.46	
	Flounder	0	....	
	Sheepshead	....	....	
	Total	991		
March 5″ Net	Drum	90	90.19	
	Redfish	9	9.09	
	Total	99		
March 3″ Net	Drum	429	81.40	
	Redfish	43	8.16	
	Trout	55	10.44	
	Total	527		
April 5″ Net	Drum	26	52.00	
	Redfish	2	4.00	
	Trout	22	44.00	
	Total	50		
April 3″ Net	Drum	88	88.00	
	Redfish	0	....	
	Trout	12	12.00	
	Total	100		
October 5″ Net	Drum	192	96.97	
	Trout	4	2.02	
	Flounder	1	.51	
	Sheepshead	1	.51	
	Total	198		
November 5″ Net (3 days fishing only)	Drum	42	71.2	89.8%
	Sheepshead	11	18.6	
	Trout	5	8.47	
	Redfish	1	1.70	
	Total	59		
December 5″ Net	Drum	212	92.8	98.9%
	Sheepshead	14	6.1	
	Trout	0	....	
	Redfish	1	.55	
	Flounder	1	.55	
	Total	228		

Table 9—Continued

Catch of Food and Games Fishes with Various Commercial Type Nets

	Year of 1955			
January 5″ Net	Drum	135	96.4	97.8%
	Sheepshead	2	1.43	
	Trout	2	1.43	
	Redfish	1	.72	
	Total	140		
February 3¾″ Net	Drum	43	71.66	
	Redfish	15	25.00	
	Trout	2	3.34	
	Total	60		
February 7″ Net—3 days	Drum	35		
	Sheepshead	2	Average 10# each	
	Total	37		
	Year of 1952 5″ Gill Net Only			
June	Drum	180	95.3	
	Redfish	1	.55	
	Trout	5	2.6	
	Flounder	3	1.55	
	Total	189		
July	Drum	199	96.1	
	Redfish	0	....	
	Trout	6	2.9	
	Flounder	2	1.0	
	Total	207		
August	Drum	266	90.5	
	Redfish	2	.6	
	Trout	19	6.5	
	Flounder	2	.6	
	Sheepshead	5	1.8	
	Total	294		
September	Drum	138	100	
October	Drum	212	95.5	
	Redfish	0	.....	
	Trout	1	.45	
	Flounder	5	2.25	
	Sheepshead	4	1.80	
	Total	222		
November	Drum	466	96.1	
	Redfish	3	.62	
	Trout	1	.21	
	Flounder	9	1.86	
	Sheepshead	6	1.24	
	Total	485		
December	Drum	434	91.5	
	Redfish	17	3.58	
	Trout	10	2.11	
	Flounder	8	1.69	
	Sheepshead	5	1.07	
	Total	474		

RELATIONSHIP OF WINDS AND CURRENTS TO THE BIOTA

Fish and crustaceans normally moved against the wind, and, therefore, against the tides. When the wind was in one direction and the tide in an opposite direction most fish milled around in the water with no definite pattern of movement. Eddies were normal at this time on the flats south of the causeway and between openings of spoil banks. Silt, carried by water, was dropped at these points; occasionally siltation was heavy enough to kill submerged vegetation. This same situation occurred in coves near spoil banks, and the bottom of these coves was usually very silty.

When Baffin Bay was affected by wind currents the upper Laguna Madre was affected also. Strong northerly winds drew water and sometimes fauna out of Baffin Bay and moved it toward and through the landcut. Strong southerly winds reversed this process pushing water out of Baffin Bay and sweeping it northward. Because this secondary bay was often more saline than the lagoon proper, these currents contributed to the hypersalinity in the lagoon. Fish were plentiful in this saline discolored water from Baffin Bay, but were difficult to catch on rod and reel. Many fish congregated north and south of this "red water." Motile invertebrates normally moved ahead of this hypersaline block. During winter months this block was located between Baffin Bay and the causeway. Less saline water, in summer, moved northward through the landcut, and many fish milled around in that area.

Summary

The upper Laguna Madre is a long narrow lagoon characterized by shallow flats, noted for hypersalinity, heavy fish populations, and discolored water. No true reefs are present but serpulid "rock" is plentiful near Baffin Bay. Reddish water may be caused by several factors:

Dissolved iron compounds, decaying vegetation with poor water circulation, Phytoplankton, and possible clay deposits.

The average depth of the area is three feet; the average width is four miles. At the northern end water flow is restricted by an earth-fill causeway; on the south a similar restriction is caused by a large bar. Thus the area is similar to a lake. The watershed is small and waterflow into the area is limited to creeks in the Baffin Bay area. Padre Island on the east and desolate rangeland on the west prevent utilization of the area from land, but nmerous boats plied the water.

Periodically fish have been killed by extremely cold weather and by hypersalinity. The Intracoastal Waterway, finished in 1948 and extending the length of the lagoon, has practically eliminated mortality caused by hypersalinity.

Water temperature over a four year period has ranged from 4° to 35° C. The average minimum and maximum temperatures for each year of the survey were about 15° and 30° C. respectively.

Salinity prior to the dredging of the Intracoastal Canal reached 113.9‰. The highest salinity recorded after completion of this project was 79.0‰. Water of high salinity and that of lower salinity did not mix well. The water of higher salinity moved as a block with prevailing winds and tides. Salinity was in direct ratio to local rainfall, particularly torrential rainfall in September and October.

Many attempts have been made to open passes from the Gulf to the lagoon. All have been failures. Each pass closed quickly at the Gulf entrance and water that entered did not mix well with the water of the lagoon.

The area is generally windy with a prevailing southeasterly wind during all summer months, which sometimes attained velocities of 50 miles per hour. The primary importance of wind action lay in its effect on movement of waters of different salinities and the resultant effect on flora and fauna. Generally northerly winds lowered the tide in the northern section and raised it in the southern. Southerly winds reversed this action.

Heavy rainfall has been very important to the area. Rainfall of 15 inches or more in September and October prevented salinity from rising much above 55‰ the following year. Smaller quantities of rainfall resulted in summer salinities of 65–70‰.

Lower forms of vegetation were not plentiful in this hypersaline area. Phytoplankton was practically non-existent in salinities above 60‰.

Members of the phyla Protozoa, Porifera, Platyhelminthes, Nemathelminthes (except planktonic species) and Trochelminthes were all rare in the area, being limited by excessive salinity. Coelenterates were somewhat limited in hypersalinity. Ctenophores were plentiful at the highest salinity recorded. Polychaetes were abundant at most salinities and provided food for many forms.

Two euryhaline copepods were present. *Acartia tonsa* (Dana) was extremely abundant between 47–75‰. *Metis japonica* (Edwards) was always present but seldom abundant. Both spawned in the area.

Several parasitic copepods were present but were limited by salinity above 40‰.

Two forms of barnacles were extremely abundant at all levels of salinity but spawned only below 45‰.

Isopods were rare not being tolerant of hypersalinity.

Amphipods were exceedingly numerous throughout the area in salinities of 50‰ or less and spawned in the area.

Penaeid shrimp of three species were present in the area but only *P. aztecus* (Ives) withstood salinity above 45‰. None tolerated salinity much above 60‰.

Only four species of bivalves were present; *Anomolocardia cuneimeis* (Say), was abundant at salinities between 35–50‰; *Mulinia lateralis* (Conrad) was present but seldom abundant; *Polymesoda floridana* and *Telina texana* (Conrad) are similar in scope. Gastropods were very scarce.

As the salinity increased, the number of species decreased; the number of individuals of each available species increased up to the optimum which is usually around 45‰ and 25° C. In many instances the average size of the vertebrate individual increased with the salinity increase, while the average size of the invertebrate individual decreased.

A total of 22 faunal species tolerated salinity of 75‰. Eighteen additional species withstood salinity to 60‰; fifty-one more species were limited if the salinity was above 45‰; and twenty-one species were not tolerant of salinity above 30–35‰.

In general high salinity and high temperature coincided. In a few cases where high salinity and low water temperature coincided it was found that various forms tolerated a much higher salinity than they normally could.

Tidal effects on salinity were not notable except for the moving of a hypersaline "block" from one end of the lagoon to the other.

High salinity over a period of several months completely eliminated widgeongrass and restricted growth of shoalgrass.

Vegetation played an extremely important role in the ecology of the area. Many forms lived in this vegetation, others spawned in it, still others ate it. Man and the black drum were both destructive to this vegetation; man by dredging and dragging, black drum by digging for food. The causeway may have been responsible for more rapid than normal siltation and sedimentation.

If present drouth continues, this rapid siltation may cause the upper eight miles of the Laguna Madre to become dry land within twenty-five years.

LITERATURE CITED

Anderson, A.W. 1949. Water samples in northern Laguna Madre, July 7, 1949. *Texas Game and Fish Comm. Ann. Rept.*, 1948–1949.

Baker, B. B. 1949. Compilation of Salinity Data from the Laguna Madre. *Texas Game and Fish Comm. Ann. Rept.*, 1948–1949.

Breuer, J. P. 1957. An ecological study of Baffin and Alazan Bays. *Publ. Inst. Mar. Sci. Univ. Texas,* 4(2):

Bullard, Fred M. 1942. Source of beach and river sands on gulf coast of Texas. *Bull. of the Geological Society of America,* 53: 1021–1044.

Burkenroad, M. D. 1951. Some principles of marine fisheries biology. *Publ. Inst. Mar. Sci. Univ. Texas,* 2 (1): 181–212.

Burr, J. G. 1930. A sail down the Laguna. *Year Book on Texas Conservation of Wildlife,* 1929–1930, Texas Game, Fish and Oyster Comm., Austin, 54–58.

Collier, Albert, and Hedgpeth, Joel W., 1950. An introduction to the hydrography of tidal waters of Texas. *Publ. Inst. Mar. Sci. Univ. Texas,* 1 (2): 121–194.

Gunter, Gordon. 1945a. Studies on marine fishes of Texas. *Publ. Inst. Mar. Sci. Univ. Texas,* 1 (1): 1–190.

————. 1945b. Some characteristics of ocean waters and the Laguna Madre. *Texas Game and Fish,* 3 (1): 7, 19, 21, 22.

————. 1950. Seasonal population changes and distributions as related to salinity of certain invertebrates of the Texas coast, including the commercial shrimp. *Publ. Inst. Mar. Sci. Univ. Texas,* 1 (2): 7–51.

————, and Henry Hildreband. 1951. Destruction of fishes and other organisms on south Texas coast by the cold wave of January 28–February 3, 1951, *Ecology,* 32 (4): 731–736.

Hartman, Olga. 1951. The littoral marine annelids of the Gulf of Mexico, *Publ. Inst. Mar. Sci. Univ. Texas,* 2 (1): 7–125.

Hedgpeth, Joel W. 1947. The Laguna Madre of Texas. *Trans. Twelfth N. Amer. Wildl. Conf.,* 364–380.

————. 1953. An introduction to the zoogeography of the north-western Gulf of Mexico with reference to the invertebrate fauna. *Publ. Inst. Mar. Sci. Univ. Texas,* 3 (1): 109–224.

Ladd, Harry S. 1951. Brackish-water and marine assemblages of the Texas coast with special references to mollusks. *Publ. Inst. Mar. Sci. Univ. Texas,* 2 (1): 129–162.

Parker, Robert H. 1955. Changes in the invertebrate fauna, apparently attributable to salinity changes, in the bays of central Texas. *Jour. of Paleont.* 29: 193–211.

————. 1956. Macro-invertebrate assemblages as indicators of sedimentary environments in east Mississippi Delta region. *Bull. Amer. Ass. Petrol. Geol.,* 40: 295–376.

Pearse, A. S. 1951. Parasitic crustacea from the Texas coast. *Publ. Inst. Mar. Sci. Univ. Texas,* 2 (2): 5–43.

Pearson, John G. 1929. Natural history and conservation of the redfish and other Sciaenids on the Texas coast. *Bull. U.S. Bur. Fish,* 44 (1928): 129–214.

Pulley, T. E. 1952. An illustrated check list of the marine mollusks of Texas. *Tex. Jour. Sci.,* 4 (2): 167-199.

U.S. Dept. of Interior, Fish and Wildlife Service. 1954. Gulf of Mexico, its origin, waters and marine life. *Fish. Bull.,* U.S., 55: 1–604.

Studies of the Ecology of Two Species of *Donax* on Mustang Island, Texas

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Introduction

The data presented in this paper are the results of an ecological study of two species of *Donax* on Mustang Island, Texas, with supplementary observations at Grand Isle, Louisiana. This little clam is of interest for several reasons. First, it forms the basis for a small fishery which is intermittently important in various parts of the world. Second, some species of *Donax* are known for enormous populations which develop periodically and then suddenly collapse. Following a period of great abundance is often a period of extreme scarcity. Also, the genus is almost unique in its ability to develop and maintain populations on a wave-swept beach. This adaptation to the conditions on beaches, subject to surf pounding and the consequent grinding action of sand, and the ability of the clam to migrate shoreward and seaward synchronous with the tide are items of great interest from an ecological viewpoint.

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This investigation, having as its objective the accumulation of knowledge of the basic conditions under which the local northern Gulf species live, was originally begun at the suggestion of Dr. Gordon Gunter and Mr. Martin D. Burkenroad and was continued under the direction of Dr. J. G. Mackin.

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HISTORICAL DISCUSSION

Most papers concerning *Donax* are of European origin. Many treat primarily the relations of certain larval trematodes to the host mollusc. Leidy (1879), Giard (1897 and 1907), Rees (1939), and Pelseneer (1896) are authors of the leading papers concerning the parasites of *Donax*.

Orton (1929) estimated that one hundred million *D. vittatus* (DaCosta) died in a three mile stretch of coastline in England. Coe (1953) reports that there were seven resurgent populations of *D. gouldi* Dall on the coast at La Jolla, California since 1894. After the death of the population in 1938 he could find not a single individual for six months.

Williams reported an alga, *Enteromorpha flexuosa* (Wulfen) attached to the posterior end of *Donax* shells from the coast of North Carolina. The alga found growing on the *Donax* shells on Mustang Island, Texas, is the same species identified by Dr. Harold Humm of Florida State University.

MacGinitie and MacGinitie (1949) reported that the California species of *Donax* often have a hydroid, *Clytia bakeri,* attached to the posterior edge of the shells. A closely related or identical hydroid was found attached to many of the *D. variabilis* over 15 millimeters long on Mustang Island, Texas.

The ecological study of the sand beaches at Beaufort, North Carolina by Pearse, Humm, and Wharton (1942) indicated that *D. variabilis* probably lives only one year.

Haas (1940) said that *D. variabilis* is the only mollusc that succeeds in establishing itself in the rough tide zone at Sanibel Island, Florida. Mori (1938 and 1950) reported on the ecology of *D. semignosus* (Dunker) on the coast of Japan. This clam migrates shoreward at flood tide and retreats offshore at ebb tide. The distance of migration is 3 to 6 meters at neap tide and often over 30 meters at spring tide. He said the motivating stimulus on a flood tide is the shock or vibration given the sand when the waves beat the shore. The stimulus on an ebb tide is the water running over the siphon tubes. This species of *Donax* has habits very similar to those observed in *D. variabilis* on the Texas coast.

Johnson (1934) listed the following species of *Donax* as occurring on the Texas coast: *D. variabilis, D. tumida, D. roemeri, D. texasiana,* and *D. denticulata.* Pulley (1952) in commenting on Johnson's list states that *D. roemeri* is probably a synonym of *D. texasiana* and is the most common species of *Donax* on the Texas beaches. He also says that all except *D. denticulata* may be subspecies of *D. variabilis.*

As for commercial use, Talavera (1933) listed *Donax* as one of the edible molluscs of Manila. Coe (1953) said that on the California coast *D. gouldi* are often scooped up as they lie on top of the sand and used in making clam broth. At times this is done commercially. No commercial fishery exists in Texas, though the clams seem to be plentiful enough during some summers to support such a fishery. The clams are used by many people on Mustang Island in the preparation of a broth of very good flavor.

In Florida cemented deposits of *Donax* shells are extensively mined and the "coquina rock" is used as building stone and for roads.

METHODS

Most of the observations were made on the Gulf beach of Mustang Island near Port Aransas in Nueces County, Texas. The inset on Figure 1 shows the general location. The five stations visited regularly are numbered on the map.

Samples were taken from these five stations at monthly intervals from June to September 1951. Later, samples were taken intermittently until June 1952. A sample from a station consisted of three sub-samples of Donax from one concentration. One sub-sample was taken from the shoreward part of the concentration, one from the middle, and one from the seaward part. All the sand to a depth below the clams was scooped up and sieved through a screen backed with hardware cloth fastened to a wooden frame. This removed the sand, leaving all the Donax. An average sized sample contained 1500 to 2000 clams. These clams were preserved in 10 per cent formaldehyde solution.

The average area of four or five concentrations was computed and the number of concentrations per mile was counted. From the data obtained, the number of clams in a concentration, the number of clams per mile of beach, and the water displacement of the clams per mile of beach was computed. The computations for Station 2, August 3, 1951, are given as an example:

$$\frac{1\text{ mile}}{1760\text{ yards}}\quad\frac{189\text{ ft.}^2}{\text{concentrations}}\quad\frac{1430\text{ clams}}{\text{ft.}^2}\quad\frac{183\text{ concentrations}}{2.5\text{ miles}} = 11240\text{ clams/yd.}$$

$$\frac{1\text{ mile}}{1760\text{ yards}}\quad\frac{189\text{ ft.}^2}{\text{concentrations}}\quad\frac{\begin{array}{c}231\text{ cc.}\\ \text{water displace.}\end{array}}{\text{ft.}^2}\quad\frac{183\text{ concentrations}}{2.5\text{ miles}} = 1816\text{ cc. water displace./yd.}$$

Length-frequency graphs were made for each station and for all stations on each sampling date. Twenty-five clams in each size group at half-millimeter intervals from 8 to 21.5 millimeters were measured and the weight in grams of live clams, wet meat, dry meat, wet and dry shell was recorded (Table 1). Using these data along with the volume (water displacement) per mile of beach the estimated dry organic matter of *Donax* per mile of beach was computed.

Live clams were taken frequently during the summer of 1951 for examination for cercarial and precercarial trematode parasites. Field observations on the seaward and shoreward movements of *Donax* were made at all tide stages.

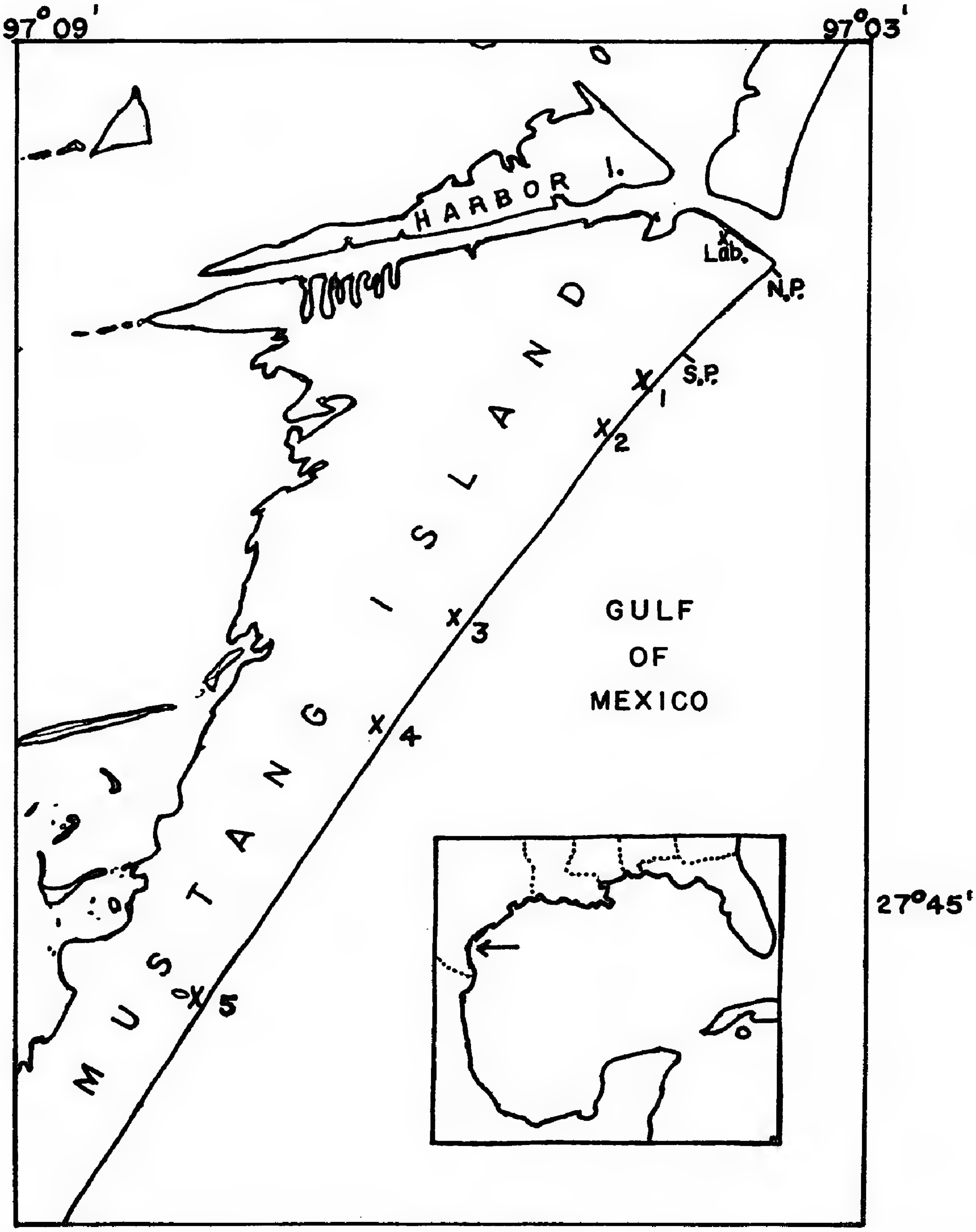
97°09'
97°03'
27°45'
HARBOR I.
Lab.
N.P.
S.P.
MUSTANG ISLAND
GULF OF MEXICO
1
2
3
4
5

Fig. 1. Location of stations. Lab., Institute of Marine Science; N. P., north pier; S. P., south pier.

The Species of *Donax* in Texas

Specimens of *Donax* from Mustang Island were sent to the United States National Museum and were identified by Dr. Harold A. Rehder as *Donax variabilis roemeri* Philippi and *D. tumida* Philippi.

Pulley (1952) identified all Donax from Mustang Island as *D. variabilis texasiana* Philippi 1847 (=*D. v. roemeri* Philippi 1849). Pulley also wrote that *D. v. tumida*

TABLE 1

Water Displacement and Wet and Dry Weights of Prescribed Numbers of *Donax variabilis* of Certain Lengths[a]

Length mm.	No. of Donax	Live Clams	Weight in Grams				Water Displacement cc.		
			Meat		Shell				
			Wet	Dry	Wet	Dry	Live Clams	Meat	Shell
8.0	25	2.4	0.48	0.14	1.9	1.8	1.7	0.4	0.9
8.5	25	3.4	0.69	0.19	2.6	2.4	2.0	0.6	1.2
9.0	25	3.8	0.73	0.21	3.0	2.8	2.4	0.7	1.5
9.5	25	4.5	0.74	0.20	3.6	3.1	2.6	0.8	1.5
10.0	25	5.2	0.87	0.22	4.0	3.3	3.1	0.9	1.7
10.5	25	6.2	0.94	0.26	4.2	4.1	3.6	0.9	1.8
11.0	25	6.3	1.00	0.36	4.5	4.3	3.7	1.0	1.9
11.5	25	7.2	1.25	0.50	5.0	5.0	4.2	1.2	2.0
12.0	25	7.9	1.10	0.51	5.5	5.5	5.0	1.2	2.4
12.5	25	9.4	1.4	0.5	6.9	6.3	5.6	1.4	2.7
13.0	25	10.5	1.9	0.6	7.5	6.9	6.3	1.7	3.2
13.5	25	11.8	2.2	0.6	8.9	8.1	6.8	2.0	3.4
14.0	25	13.1	2.3	0.6	9.8	9.1	7.7	2.1	3.9
14.5	25	14.2	2.7	0.6	10.5	9.6	8.2	2.4	4.2
15.0	25	15.3	2.8	0.6	11.2	10.6	9.0	2.6	4.5
15.5	25	17.2	2.9	0.7	12.7	11.6	9.9	2.8	5.1
16.0	25	19.1	3.3	0.7	13.9	13.0	11.2	2.9	5.5
16.5	25	19.2	3.3	0.7	14.4	13.7	12.3	2.9	6.0
17.0	25	21.1	3.5	0.8	16.7	15.8	13.0	3.1	6.7
17.5	25	22.0	3.5	0.8	18.3	16.7	15.2	3.1	7.2
18.0	25	23.7	4.3	0.9	19.3	17.9	17.2	4.2	7.7
18.5	25	26.6	4.5	0.9	19.7	19.2	18.3	4.4	7.9
19.0	25	27.9	4.7	0.9	21.4	20.0	18.3	4.7	8.5
19.5	25	30.5	5.2	1.0	23.1	21.9	19.9	5.1	9.8
20.0	25	31.6	5.8	1.1	23.6	22.9	20.2	5.4	9.3
20.5	25	34.4	6.3	1.7	25.3	25.1	21.7	5.9	9.8
21.0	25	35.1	6.5	1.1	26.0	24.3	22.7	6.0	10.0
21.5	25	36.2	6.7	0.8	25.7	25.4	23.8	5.8	11.2

[a] These *D. variabilis* were collected from Station 1 on August 18, 1951.

is a subspecies, not a species, and that the only subspecies of this type he has seen came from the Louisiana coast. The subspecies *D. v. tumida* and *D. v. texasiana* seem to intergrade around Galveston and to the east, according to Pulley, but the latter is much more common. Pulley wrote (in personal correspondence) that there are many intergradations of the species and that he would be very wary of trying to identify *Donax* species by using the amount of shell overlap as a key character, as is done in the tabulation of the differences in the species given below.

Thousands of *Donax* were examined in this investigation and most could be separated into species with the naked eye; the differences are very definite. No variations in the amount of shell overlap were noted. *D. tumida* from 2 to 15 millimeters long and *D. variabilis* from 2 to 22 millimeters long were collected from Mustang Island and no intergradation appeared in any of them. Therefore, the writer feels that Rehder's identification is correct and that there are two separate species of *Donax* found on Mustang Island.

D. variabilis and *D. tumida* are different in both form and habit. During the winter the populations mix, usually in water from knee deep to waist deep. Then during spring and early summer both groups may be found at the water's edge. On the approach of summer the two groups separate. *D. variabilis* remains at the water's edge but *D. tumida* is found only in water one to three feet deep, and possibly deeper. The outer limit was not ascertained. During the summer all *Donax* found at the water's edge were *D. variabilis* and all found in a foot or more of water were *D. tumida,* with no exceptions. From this observation, and the observation that *D. tumida* seemed to disappear gradually (Table 2), it was thought that *D. tumida* simply moved into deeper water in warm weather. However, observations at Grand Isle, Louisiana, where only *D. tumida* was found, indicate that most of the larger individuals of this species may die in late May or June.

TABLE 2

Percentages of *D. variabilis* and *D. tumida* on Various Dates

	Station									
	1		2		3		4		5	
Date of Sample	var.[a]	tum.[b]	var.	tum.	var.	tum.	var.	tum.	var.	tum.
June 27, 1951	100	0	100	0	100	0	100	0	100	0
August 3, 1951	100	0	100	0	100	0	100	0	100	0
September 3, 1951	100	0	100	0	100	0	100	0	100	0
September 27, 1951	100	0	......	..	......	..	......	..	......	..
September 29, 1951	100	0	100	0	100	0	100	0	100	0
October 27, 1951	100	0	......	..	......	..	......	..	......	..
November 17, 1951	100	0	......	..	......	..	......	..	26	74
December 15, 1951	6	94	......	..	0	100	15	85	......	..
June 2, 1952	39	61	37	63	38	62	66	37	100	0
June 27, 1952	85	15	77	23	67	33	98	2	100	0
January 19, 1953	82	18	......	..	......	..	......	..	79	21

[a] *D. variabilis.*
[b] *D. tumida.*

Clams of both species were measured with calipers for length, depth, and thickness. The length was the greatest distance from anterior to posterior of the closed clam. The depth was measured from dorsal to ventral side of the clam at the point of greatest distance. Thickness was measured from lateral to lateral over the thickest spot.

An enumeration of the differences noted between *D. tumida* and *D. variabilis* follows.

Physical Differences:

D. tumida	*D. variabilis*
1. Left valve overlaps right on ventral teeth.	1. Valves meet evenly on ventral teeth.
2. Left valve projects slightly farther than does right.	2. Left and right valve meet evenly with no projection.
3. Ridge of ventral teeth nearly same width on entire length.	3. Ridge of ventral teeth widest at head and tapers to broad end of wedge.
4. Clams over 5.5 millimeters in depth are more deeply cupped as shown in Figure 2.	4. Not as deeply cupped or thick for same depth.
5. All specimens examined from 3 to 7 millimeters long were sexually mature.	5. Thirty-two specimens from 3 to 11 millimeters long were immature; mature males and females 4 millimeters long were found.

Habitat Differences:

1. During summer this species is found in knee-deep or deeper water.	1. During summer this species is found at water's edge or slightly above.
2. Major die-off seems to occur in May and is of short duration.	2. Major die-off occurs in September but is not of short duration; deaths occur throughout summer.
3. Peak of set seems to occur in November and late June.	3. Peak of set seems to occur in October and May.

The depth-thickness ratio as given in Table 3 is less for *D. variabilis* than it is for *D. tumida* until the 8.2 millimeter length is reached and then the ratio is larger for *D. variabilis.* The length-thickness ratio is larger in *D. variabilis* for all sizes above 8.2 millimeters but is approximately the same for those under 8.2 milimeter. The length-depth ratio for the two species is approximately the same.

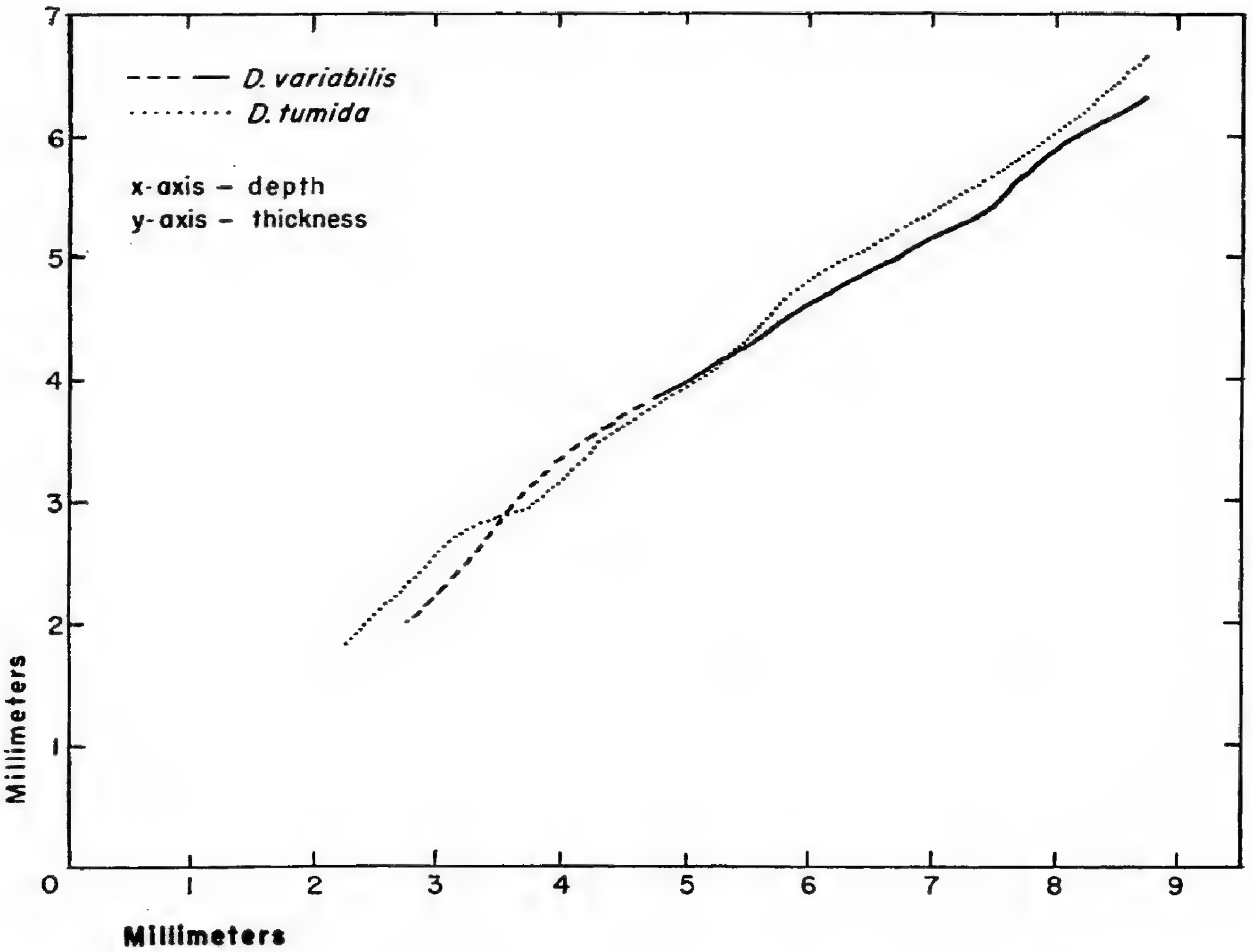

FIG. 2. Graphs comparing depth vs. thickness of *D. tumida* and *D. variabilis.*

TABLE 3

Length-Depth-Thickness Ratios Comparing *D. variabilis* and *D. tumida*

Length in mm. Size Interval	*D. variabilis*				*D. tumida*			
	No.	Length/Depth	Length/Thickness	Depth/Thickness	No.	Length/Depth	Length/Thickness	Depth/Thickness
2.3– 3.2	....	......	......	......	50	1.34	......	1.36
3.3– 4.2	....	......	......	......	50	1.33	1.65	1.24
4.3– 5.2	....	......	......	......	50	1.44	1.72	1.20
5.3– 6.2	1	1.58	1.94	1.23	37	1.43	1.85	1.29
6.3– 7.2	2	1.50	1.89	1.26	32	1.47	1.90	1.30
7.3– 8.2	30	1.50	1.93	1.28	48	1.50	1.99	1.32
8.3– 9.2	43	1.50	2.02	1.34	51	1.51	2.01	1.33
9.3–10.2	48	1.56	2.05	1.32	50	1.54	1.99	1.30
10.3–11.2	55	1.57	2.13	1.36	50	1.57	2.07	1.32
11.3–12.2	41	1.59	2.22	1.40	50	1.61	2.12	1.32
12.3–13.2	47	1.59	2.19	1.38	50	1.63	2.17	1.33
13.3–14.2	48	1.64	2.23	1.36	34	1.63	2.16	1.33
14.3–15.2	49	1.63	2.26	1.38	4	1.63	2.12	1.29
15.3–16.2	50	1.63	2.29	1.41	2	1.67	2.26	1.35
16.3–17.2	48	1.63	2.32	1.42	....	......	......	......
17.3–18.2	51	1.64	2.34	1.43	....	......	......	......
18.3–19.2	56	1.65	2.38	1.44	....	......	......	......
19.3–20.2	47	1.70	2.47	1.46	....	......	......	......
20.3–21.2	35	1.69	2.49	1.47	....	......	......	......
21.3–22.2	7	1.71	2.59	1.52	....	......	......	......
22.3–23.2	2	1.70	2.56	1.50	....	......	......	......

A graphic depiction of thickness versus depth of the two species is shown in Figure 2. Of those clams over 5.5 millimeters long, all *D. tumida* had a greater thickness than the *D. variabilis* for the same depth. A comparison of depth versus length and of thickness versus length of the two species is shown in Figure 3. *D. tumida* is thicker for any length above 8.5 millimeters than is *D. variabilis.* The length and depth relationship for the two species shows no apparent difference. These graphs represent 423 *D. variabilis* and 477 *D. tumida.*

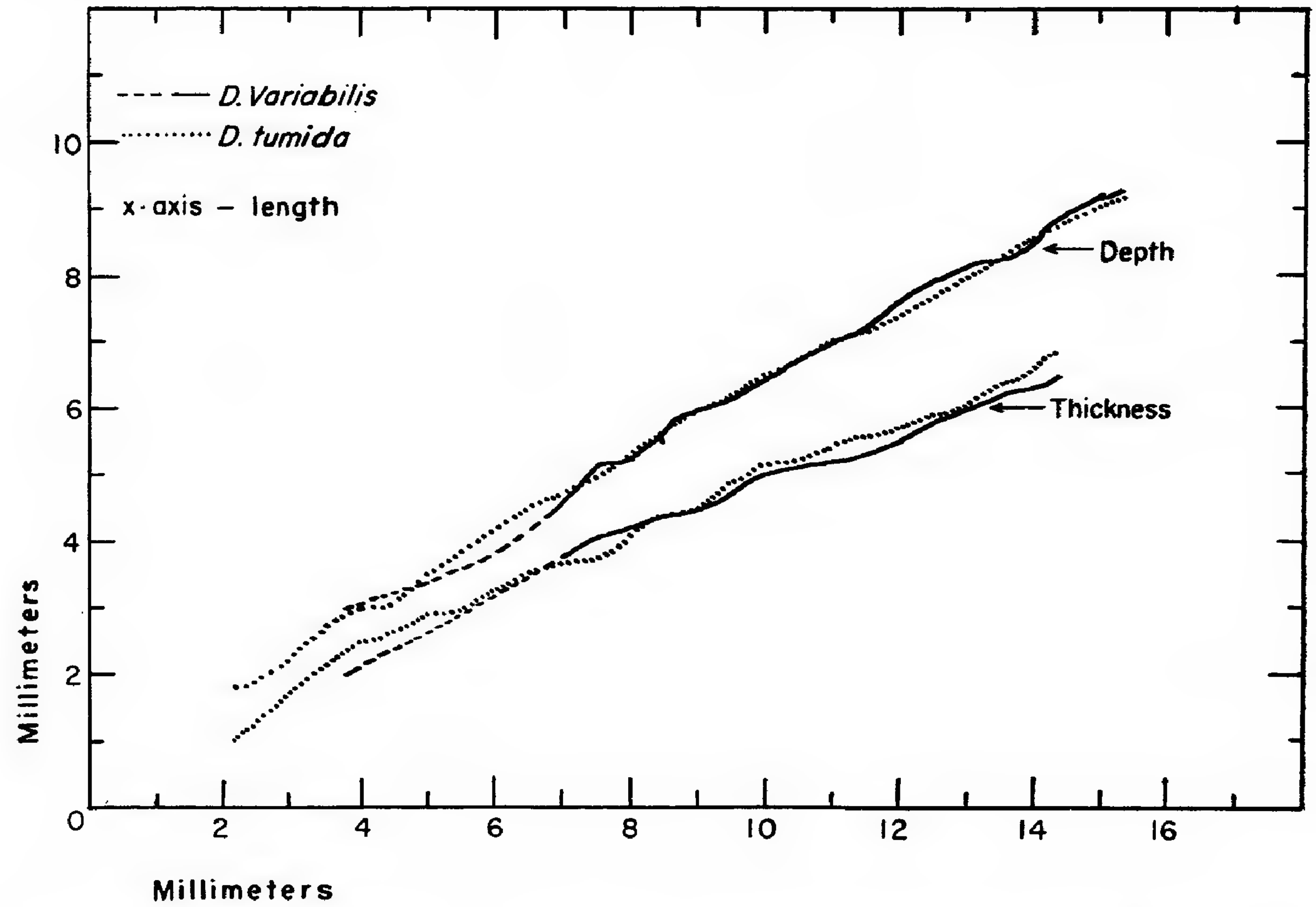

FIG. 3. Graphs comparing length vs. depth and length vs. thickness of *D. variabilis* and *D. tumida.*

HABITAT AND MIGRATIONS

During the summer the shoreline at Mustang Island consists of a series of cusps and intercusps. It is in the intercusps that the majority of the *Donax* are found. There are on the average about sixty cusps per mile, varying with the time of year. A concentration was generally found in each intercusp. The number of concentrations of *Donax* per mile of beach at different times of the year is given in Table 4.

When *Donax* are only slightly buried, they can be located by their excurrent and incurrent siphon tube holes in the sand. These two holes are about half as far apart as the length of the clam.

Donax are among the few animals that have become adapted to the wave impact area where the land meets the sea. As the tide rises and falls *D. variabilis* moves up and down the beach slope synchronous with the tide. As the clams have no independent means of locomotion other than an ability to dig in or out of sand, they hitch a ride by using the movement of the water in a wave. Within the short period of one wave the entire population, both lower and upper limits, may change its location by as much as ten yards, or

TABLE 4

Concentrations of *Donax* Per Mile

Date	Stations 1	2	3	4	5	Average
June 27, 1951	......	......	......	......	......	55
August 3, 1951	110	73	71	75	51	80
September 3, 1951	......	......	71	70	50	64
September 29, 1951	14	14	15	14	14	14
November 17, 1951	Not concentrated, scattered					....
December 16, 1951	Not concentrated, scattered					....
June 2, 1952	Not concentrated, in bands 1 to 1.5 yds. wide					....
June 27, 1952	71	65	61	57	52	59

it may not move at all. One change in position from inshore to offshore by one clam was observed to be 24 yards. After riding a wave the clam buries in 1.5 to 3 seconds with ten to twenty probing movements. The movements are slower in winter. The size of the clam has no effect on the time or on the number of movements required to bury.

On a rising tide *D. variabilis* appears to be influenced by the vibrations of the breaking waves transmitted through the sand. When the clams are at the height of a rising period they can be made to rise by running a jeep about 20 yards or nearer the population. As the jeep runs along the beach parallel with the water's edge, the clams rise just about even with the jeep. The picture in Figure 5, which shows a heavy concentration of *Donax* lying on the beach, was made after inducing the clams to rise to the false stimulus of a jeep.

On a falling tide *D. variabilis* rises after a wave breaks over the sand. It was noted that just before the population pops to the top of the sand the clams are flush with the

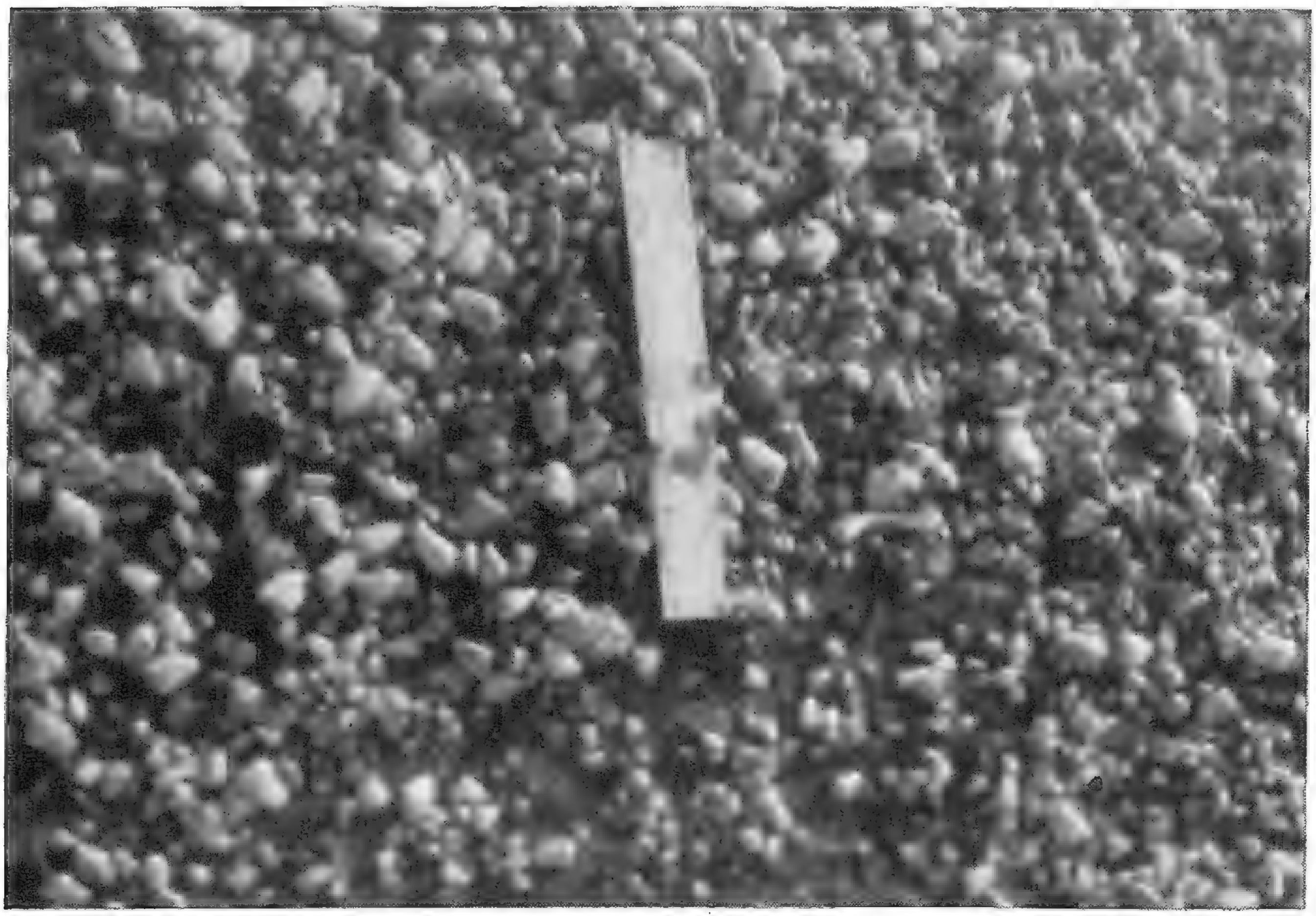

FIG. 5. *D. variabilis* on Mustang Island, Texas, Station 1.

surface. Perhaps after a certain amount of sand has been removed from the top of the buried clams they rise. When the velocity of the water decreases because of the lesser inclination of the beach the clams bury themselves deeper, up to about 20 millimeters deep, with a little circlet of sand raised about them. When the clams are thus buried the siphon tube holes are not visible. Occasionally clams are trapped high enough above low tide to be run over by passing automobiles, as much as fourteen yards from the water. The majority of these trapped clams apparently survive and rejoin the population because no damaged clams could be found the day after several trapped colonies were noted and marked. During the summer *D. tumida* were found only in water where movements could not be observed.

To determine whether or not *Donax* would live in places where there was no surf action, several groups of clams were transplanted to different localities where there was no wave action. One plant was made on a coarse sandy beach on Lydia Ann Channel at the northwest end of Mustang Island. Except for the lack of wave action this location seemed ideal for *Donax*. One week after planting only one individual was found; after the second week none was found.

Four cans filled with beach sand were buried flush with the water at the edge of the channel. Some clams were put in each can. One week later all the *Donax* were dead. At the end of this week there was no apparent rust on the cans.

Live *Donax* were put into a floating live box and hung in the water under the laboratory. The mortality rate was low the first month, but no growth occurred. The second month the mortality rate was probably higher than normal, and still no growth occurred. All these transplantings would seem to indicate that the surf is necessary for *Donax* to live and grow. Mori (1938) said the clams live on minute living organisms attached to the sand grains on the beach. Material in the stomachs and guts of Texas specimens consisted of small particles including diatoms.

Drift of clams along the shore may or may not occur. To try to determine if such drift does occur a group of *Donax* with algae attached was planted a half mile south of the jetty where few of the native *Donax* had algae. The transplanted group remained at this location throughout the summer. However, this location may have been too close to the jetty to be affected by shorewise drift, if such drift does occur.

Three groups of *Donax*, measuring in volume about a half gallon each, were planted on the southeastern end of St. Joseph Island. This location is on the Gulf side of the island just north of Mustang Island, with Lydia Ann Channel between the two islands. Some dead hinged shells were also planted at the same time. A week later not one live clam or clam shell could be found. That shorewise drift moved and scattered the clams farther north along the beach is one possible explanation. Thus, of the two experiments concerning drift, one seemed to indicate that drift does not occur and the other was inconclusive.

Population Density

The total population of *Donax* was estimated by the procedures discussed in the methods section. More concentrations were found per mile of beach in early summer than at other times of the year (Table 4). With the approach of fall there were progressively fewer concentrations at all stations. In winter the population was scattered and was not grouped in concentrations.

In June, July, and August each concentration was in an intercusp. Then, on September 3 the populations at Stations 4 and 5 were found in shallow water above a very high sand bar which was probably built during a very high tide. Only a few *Donax* were found on the Gulf side of the bars. No cusps were evident later in September. Instead, gullies had formed in the places where later cusp valleys would probably form. These gullies were twelve to twenty feet wide and only inches deep. At this time the *Donax* concentrations were on the higher ground on the south side of each gully. Figure 4 is a sketch showing the condition that existed in each of the four populations examined. At this sampling on September 29 there were only fourteen concentrations per mile.

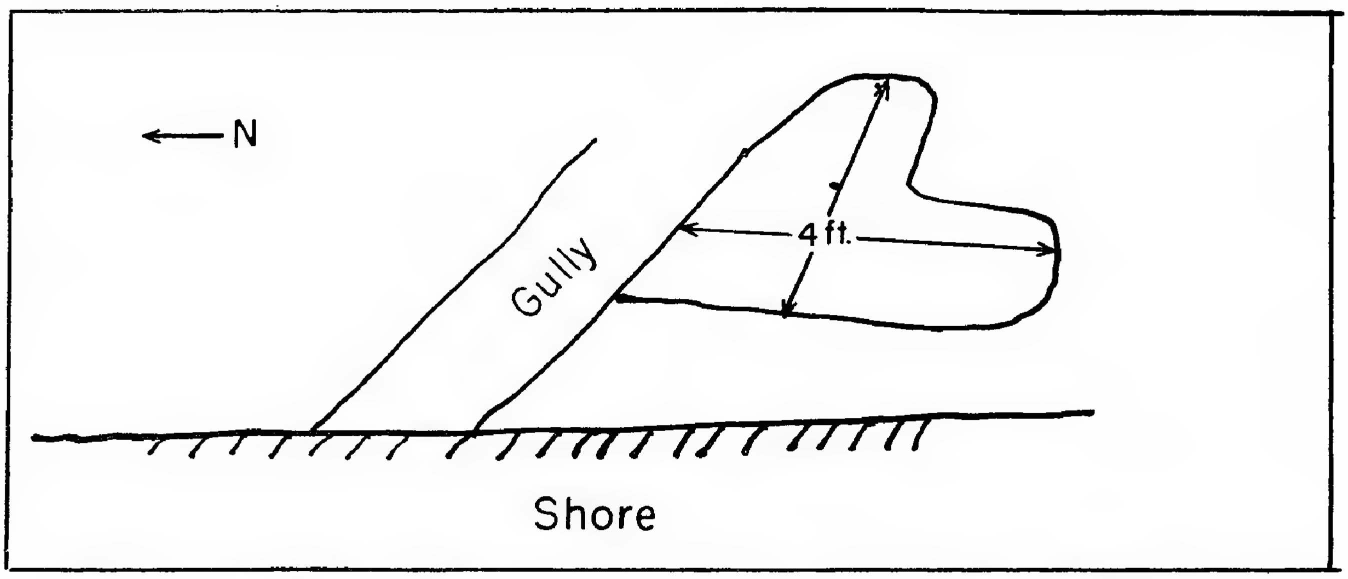

Fig. 4. Location of *D. variabilis* populations found in September 1951 on Mustang Island.

The greatest number of *Donax* per linear yard of beach was found at Stations 4 and 5 during the early summer months. During this same period, however, the greatest volume of *Donax* was found at Stations 1 and 2. At all times larger individuals were found at Stations 1 and 2 than were found at the other stations. The greatest number of clams was found in the spring, with the abundance gradually decreasing to a low in winter, suggesting that some of the clams may live for a year and others for only a part of a year.

The size of a concentration varied in width from half a foot to ten yards and in length from two yards to a continuous band along the beach. The "length" is the axis paralleling the water line.

On November 17, 1951, following a norther, most of the *Donax* were found buried 30 millimeters under the surface, with a few at shallower depths. Some were found twenty feet above the water line and others were found in knee deep water. They were so scattered that it was impossible to estimate populations. On this sampling date 74 per cent of the clams collected at Station 5 were *D. tumida.* All others collected on stations prior to this time were *D. variabilis* (Table 2).

The December 15 samples were taken after a hard norther that had brought air temperature to below freezing the night before. The shoreward limit of the *Donax* population was found in water six inches deep, where the sand temperature was 13.5° C. Sand temperature at the edge of the water was 10.6° C. The depth of the population was not ascertained. At Station 1 some large clams were found near the water's edge and it seemed as if these were attempting to get to deeper water. One was observed to be successful in the manuever. These few at Station 1 were the only clams collected at the water's edge on this date. All clams found at Station 3 were *D. tumida*, and the majority of the clams at the other stations checked were *D. tumida*.

It was estimated that more than 32,000 *Donax* were living on each linear yard of beach in the vicinity of Station 4 in June 1952. Approximately 37 per cent of these clams were *D. tumida*. This was the densest population found during the study (Table 5). The highest number of clams along the entire beach was found in June 1951 when there were an estimated 18,500 clams per linear yard of beach. This number declined to about 11,600 in August and to about 4,800 in early September 1951. At the end of September about 70 clams were found per linear yard of beach.

TABLE 5

Estimated Numbers in Thousands of *Donax* Per Linear Yard of Beach

	Stations					
Date	1	2	3	4	5	Average
June 27, 1951	8.6	7.7	21.7	23.4	31.0	18.5
August 3, 1951	5.7	11.2	4.5	16.7	20.1	11.6
September 3, 1951	....	......	7.8	4.4	2.3	4.8
September 29, 1951	0.08	0.05	0.1	0.1	0.04	0.07
November 17, 1951	Concentrations could not be determined as the holes were not visible. Population rather low and made up of small individuals.					
December 16, 1951	*Donax* in knee-deep water					
June 2, 1952	10.4	9.5	6.9	32.2	18.2	15.4
June 27, 1952	5.8	1.9	6.2	10.7	13.4	7.6

The volume and weight of *Donax* per linear yard of beach varied in proportion to the number of clams found (Table 6 and Table 7). Thus, in June 1952 at Station 4 the *Donax* had a water displacement of 5.4 liters per linear yard of beach. The average water displacement of the clams all along the beach was 1.9 liters in June 1951. This decreased to 0.02 liters per yard in late September.

TABLE 6

Estimated Volume (Water Displacement in Liters) of *Donax* Per Linear Yard of Beach

	Stations					
Date	1	2	3	4	5	Average
June 27, 1951	2.4	2.5	1.4	1.4	1.6	1.9
August 3, 1951	1.7	1.8	0.5	1.5	1.3	1.3
September 3, 1951	......	......	1.0	0.5	0.2	0.6
September 29, 1951	0.03	0.01	0.01	0.01	0.04	0.02
November 17, 1951		Scattered too much to estimate				
December 16, 1951		Scattered too much to estimate				
June 2, 1952	2.0	1.7	1.3	5.4	1.1	2.3
June 27, 1952	0.1	0.3	0.7	0.9	1.1	0.6

Mortality

If the time that shells of dead clams remain hinged could be accurately determined, fairly accurate mortality estimates could be made by counting the hinged shells. In an attempt to determine the length of time the hinges held the shells together after the clam dies, a gallon of hinged shells was placed high on the beach at Station 1. At this undisturbed place the hinges remained intact for several months and were still intact when the writer left the island.

TABLE 7

Estimated Dry Weight of Meat and of Shell in Grams Per Linear Mile of Beach

Date	Stations					
	1	2	3	4	5	Average
Meat:						
June 27, 1951	422	440	246	246	282	327
August 3, 1951	299	317	88	246	229	236
September 3, 1951	......	......	176	88	35	100
September 29, 1951	5.3	1.8	1.8	1.8	7.0	3.5
November 17, 1951	Concentrations could not be determined.					
December 16, 1951	Concentrations could not be determined.					
June 2, 1952	352	229	229	950	154	405
June 27, 1952	18	53	123	158	194	109
Shell:						
June 27, 1951	8,018	8,360	4,654	4,654	5,358	6,346
August 3, 1951	5,591	6,023	1,672	4,654	4,351	4,351
September 3, 1951	.. .	.. .	3,334	1,672	665	2,014
September 29, 1951	103	34	34	34	133	66
November 17, 1951	Concentrations could not be determined.					
December 16, 1951	Concentrations could not be determined.					
June 2, 1952	6,688	5,681	4,351	18,050	3,686	7,695
June 27, 1952	334	1,007	2,337	3,002	3,686	2,014

Hinged shells were placed on the edge of a tide pool at two places and on higher ground at another place. It was found here that those near the water broke up and were carried away much sooner than those high and dry, but still possibly not as fast as they would be had they been exposed to the surf. In the surf, beaten by the waves, it is assumed that hinged shells remain intact for only short periods, measured in weeks or days.

The great abundance of clams found on Mustang Island in June 1951 decreased gradually until August. Then the decrease accelerated and from September 3 to 29, 98.5 per cent of the population disappeared. It was observed that clams found in November and December were widely scattered. This particular disappearance may have been due to the dispersal of clams. However, more hinged shells were found during this period than at any other time, so some must have died.

A spectacular die-off of *D. tumida* was observed at Grand Isle, Louisiana, where observations were made from May 29 to June 2, 1952. On May 29 hinged shells were becoming apparent. In eleven yards of beach 74 hinged shells plus 17 pairs of shells containing rotted meat were counted. In twenty yards of beach twelve blue crabs were observed eating the meat of these dead *Donax*. The clam population was in a solid band about one and a half yards wide.

On June 2 many dead, hinged *Donax* were present on the Grand Isle beach. The shells were cast up in windrows. One handful from the water, the lowest windrow, yielded 22 pairs of empty hinged shells and 14 pairs of shells that still contained rotted meat. Two to three parallel windrows lined the beach here. The shells were just partly opened and appeared not to have been transported very far by the water. The windrows extended for at least five miles along the beach, not as continuous bands but in strips one and a half feet wide and spotty, with as much area between spots as contained in the spots. The spots varied from one to six feet long. Photographs of these are shown in Figure 6. Live *Donax* were still plentiful at this time.

Smears from 121 *Donax* taken during the Grand Isle die-off were examined under a compound microscope. Only one had a trematode cercaria, Type "A". All had meta-

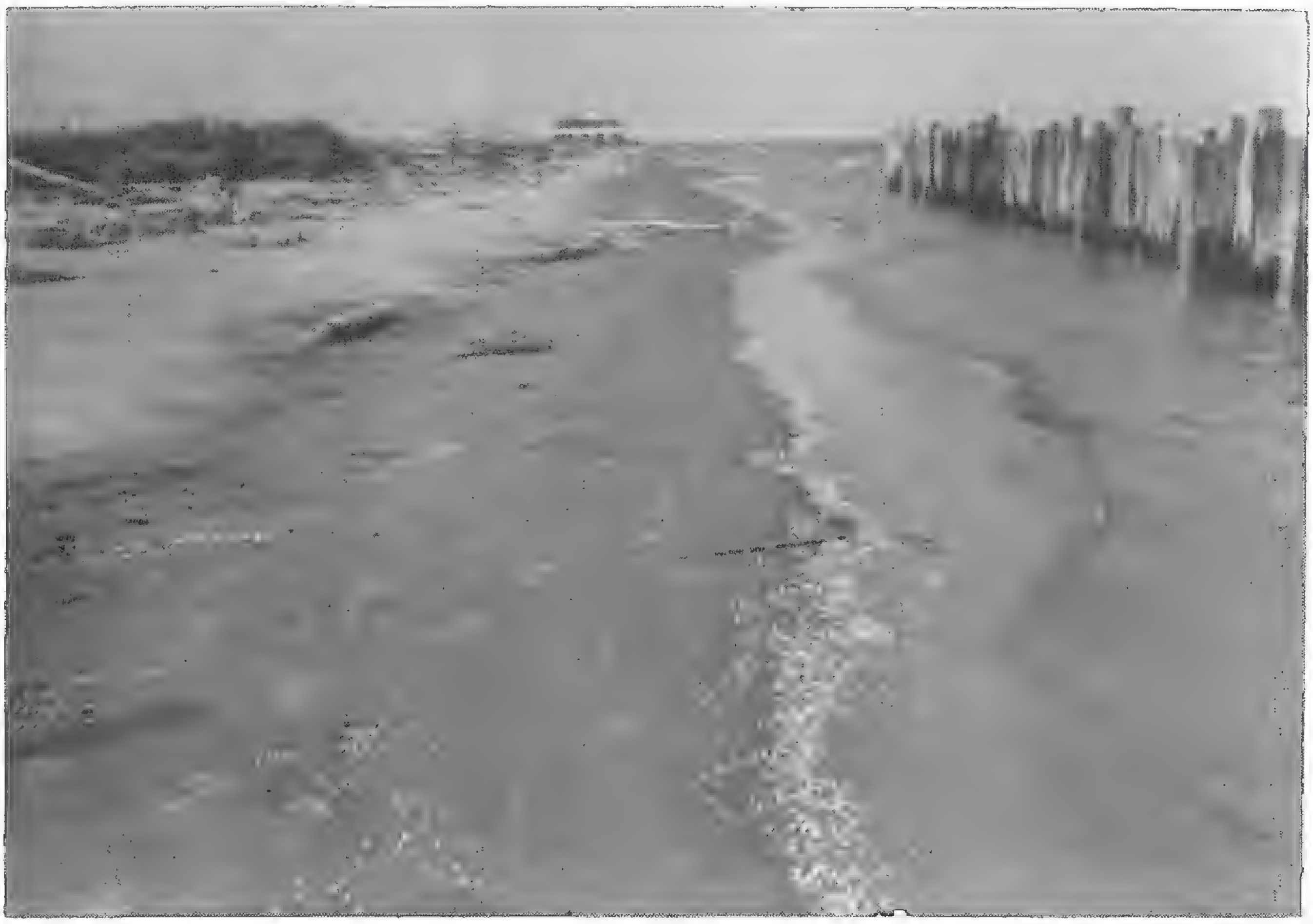

FIG. 6. Windrows of hinged shells of *D. tumida* taken during a spectacular die-off in late May 1952 at Grand Isle, Louisiana.

cercariae, as did those on the Texas coast. A protozoan that looked very much like a *Trichodina* was common around the siphon tubes.

A month later, on July 7, 1952, very few *Donax* could be found on Grand Isle. The largest *Donax* found there then was 4.5 millimeters long and most were from 3 to 4 millimeters long.

In the summer of 1951 Dr. Sewell H. Hopkins checked the beach at Grand Isle for *Donax;* he could find only small ones and they were few in number. Thus, during the summers of both 1951 and 1952 *Donax* were very scarce on Grand Isle.

Predators

A number of birds, fishes, and invertebrates eat *Donax* regularly. A list of predation observations is given in Table 8.

Stomach analysis of the following birds did not reveal any *Donax* content: *Limosa fedoa* (marbled godwit), *Arenaria interpres* (ruddy turnstone) and *Larus atricilla* (laughing gull). Stomachs of four of the six *Catoptrophorus semipalmatus* (Eastern willet) examined contained *Donax.* The one *Squatarola squatarola* (black-bellied plover) examined contained *Donax.*

One *Crocethia alba* (sanderling) was observed at close range. The bird probed with its beak in the sand with its head completely under water. A *Donax about* 12 to 14 millimeters long was brought up. The bird rolled the clam around in its beak so that it was lengthwise and then swallowed it. Twenty minutes later the same procedure was repeated.

Two drums *(Pogonias cromis)* containing *Donax* were 24 and 20 centimeters long;

TABLE 8

Observed Predators of *Donax*

Predator	*Comments*
Birds	
Catoptrophorus semipalmatus (Eastern willet)	Stomach analysis, 4 of 6 contained *Donax*
Crocethia alba (Sanderling)	Observed eating *Donax* on beach
Squatarola squatarola (Black bellied plover)	Stomach analysis, 1 of 1 contained *Donax*
Fish	
Menticirrhus spp. (Whiting)	Stomach analysis, 1 of 5 contained *Donax*
Leiostomus xanthurus (Spot)	Stomach analysis, 2 of 6 contained *Donax*
Pogonias cromis (Drum)	Stomach analysis, 2 of 9 contained *Donax*
Crabs	
Callinectes sapidus (Blue)	Frequently observed eating *Donax*
Arenaeus cribrarius (Spotted)	Observed eating *Donax*
Ocypode albicans (Ghost)	Observed handling *Donax* at night
Boring Snails	
Thais floridana (Conch)	Observed holding *Donax;* although drilling was not observed, many drilled shells were found.
Oliva spp.	
Natica duplicata (Moonshell)	

their stomachs had volumes, by water displacement, of 2.7 and 2.8 cubic centimeters respectively. The content of each stomach was about 95 per cent *Donax.* These averaged 5 millimeters in length and ranged from 2.3 to 9 millimeters.

Though no borer was observed drilling a Donax, many drilled shells were found. *Thais floridana* (oyster drill), *Oliva sayana* (lettered olive), and *Natica duplicata* (moonshell) each have been observed holding *Donax.*

Ghost crabs *(Ocypode albicans)* have been observed sitting on the *Donax*-populated part of the beach at night. When approached with a light they ran out into the water. They were observed to drop *Donax* as they left the beach but the handling of the clams was not observed. Burkenroad (personal communication) reports that, during night observations on the ocean beach in North Carolina, ghost crabs were seen to roll *Donax* around in their claws until they succeeded in opening the clams.

Blue crabs *(Callinectes sapidus)* were frequently observed eating *Donax.* Clams retrieved from blue crabs had been clipped off at the pointed end. During one observation 13 of 16 crabs eating *Donax* were one-clawed. It may be that injured crabs eat Donax more from necessity than by choice, when the more choice food cannot be easily caught with one claw.

Spotted crabs *(Arenaeus cribrarius)* were also observed eating *Donax,* though not as frequently as the blue crabs.

Commensals

An alga and a hydroid were noted growing on the posterior part of some *D. variabilis.* This alga and hydroid are commonly called commensals as they use the clam as an anchor in the surf. Strictly speaking, however, they may be considered mutualistic, as it was found that *Donax* having growths of either algae or hydroids were less frequently infested by cercarial or precercarial parasites. As shown in Table 9, *Bucephalus* and *Gymnophallus* cercariae were found in 0.6 and 1.6 per cent respectively of the clean clams in the 16 to 23 millimeter size group, but were not found in any of the 333 clams examined that were harboring algae or hydroids. No data are available as to the methods by which the algae and hydroids protect the clams from parasitism by the trematodes.

TABLE 9

Incidence of Sex, Castration, and Cercarial and Precercarial Trematode Parasites in Three Groups of *Donax variabilis*

	(1) Clean						(2) Hydroids				(3) Algae			
Size in mm.	Male	Female	Castrates A[a]	B[b]	G[c]	Total	Male	Female	Castrate A[a]	Total	Male	Female	Castrate A[a]	Total
16	15	12	0	0	0	27	4	14	0	18	5	4	0	9
17	28	30	1	0	1	60	23	26	1	50	4	11	0	15
18	59	60	4	1	2	126	30	26	2	58	10	23	2	35
19	81	70	5	2	1	159	31	19	0	50	22	15	3	40
20	51	36	6	0	2	95	21	9	0	30	9	7	0	16
21	14	8	1	0	1	24	6	0	0	6	3	1	0	4
22	4	1	0	0	1	6	0	1	0	1	0	0	0	0
23	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Total	252	217	18	3	8	498	115	96	3	213	53	61	5	119
Per Cent	50.6	43.6	3.6	0.6	1.6	100	53.7	44.8	1.4	99.9	44.5	51.2	4.2	99.9

[a] Trematode cercaria pictured in Figure 16, called "A" type cercaria.
[b] *Bucephalus*.
[c] *Gymnophallus*.

The green filamentous alga found growing attached to the posterior end of the shell of some *D. variabilis* was identified by Dr. Harold Humm as *Enteromorpha flexuosa* (Wulfen). It was found more frequently on the larger clams and only rarely on those under 15 millimeters long. The larger clams not only offer a greater area on which the alga may start growing, but also a longer time in which to become attached. Table 10 is a tabulation of 1192 *D. variabilis* collected at Station 1 on June 27, 1951 and is representative of the frequency of the occurrence of algae on the clams.

TABLE 10

Algal Infestations Related to Length of *Donax*[a]

Size in mm.	Number Without Algae	Number With Algae	Per Cent With Algae
3–14	913	0	0
15	15	1	6.2
16	38	4	9.5
17	62	16	20.5
18	97	34	26.0
19	47	22	31.9
20	17	9	34.6
21	3	0	0

[a] *D. variabilis* sample collected June 27, 1951 at Station 1 and considered representative.

Hydroids were found attached to *Donax* less frequently than algae and were apparently more affected by severe weather conditions. The incidence of hydroids increased until August, 1951, when they were found on about half as many clams as held algae. After severe weather conditions in late fall the hydroids apparently were beaten off, as only stubs of the original growths could be found. None were noted on *D. tumida*, and no hydroids found on *D. variabilis* during the winter.

Growth

In order to measure growth samples of *Donax* spp. were taken at intervals from each of the five stations marked on the map (Figure 1). In an attempt to get a representative sample from each station three sub-samples were taken at different distances from the water's edge. This was necessary because at times larger *Donax* were trapped first and were higher on the beach. These sub-samples were mixed in a large flat container and the portion to be measured was drawn off by taking all of a certain area in the mixing vessel.

The length of each clam in the representative sample was measured to the nearest millimeter and the length-frequency graphs shown in Figures 7 to 14 were made from these tabulations. When both *D. variabilis* and *D. tumida* length-frequencies are plotted on the same graph the *D. tumida* curve is shown by a dotted line. When both of these species are on the same graph the percentages for the two species combined add up to 100 per cent. The growth rates estimated from the peaks of the length-frequency diagrams are summarized in Figure 15.

DONAX VARIABILIS

The length-frequency graphs show in Figures 7–11 different patterns probably because each station was affected to a different degree by such factors as proximity to the jetties and the public bathing beach area. Growth alone may not be the reason for the position and rate of advance of the modes. Recruitment, mortality, and shifting of the

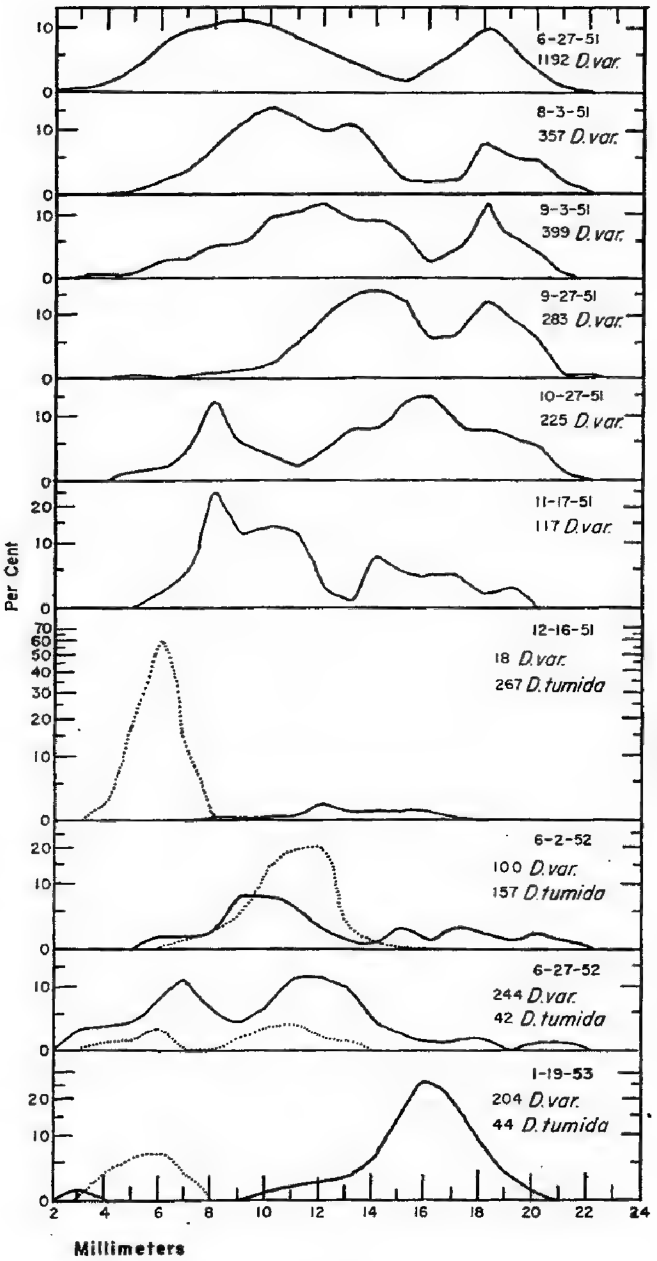

FIG. 7. Length-frequency graphs of *D. variabilis* and *D. tumida* at Station 1.

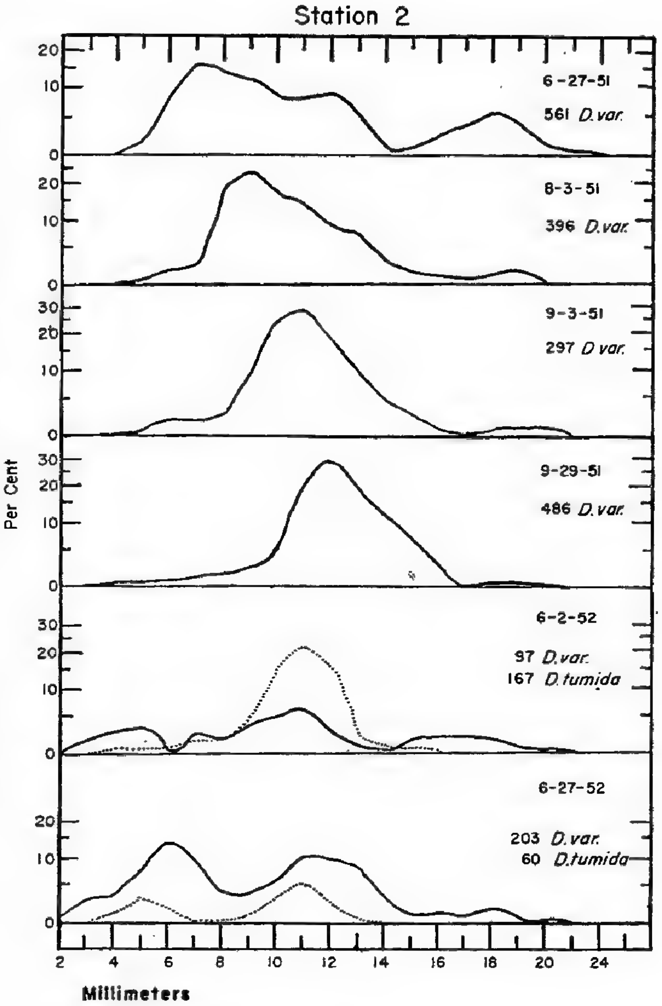

FIG. 8. Length-frequency graphs of *D. variabilis* and *D. tumida* at Station 2.

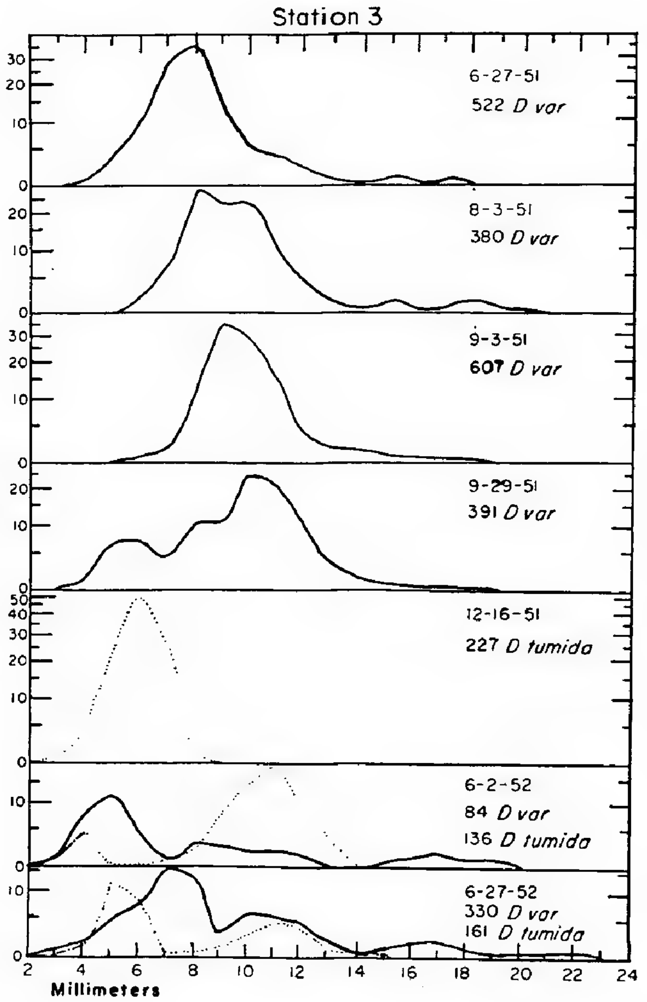

FIG. 9. Length-frequency graphs of *D. variabilis* and *D. tumida* at Station 3.

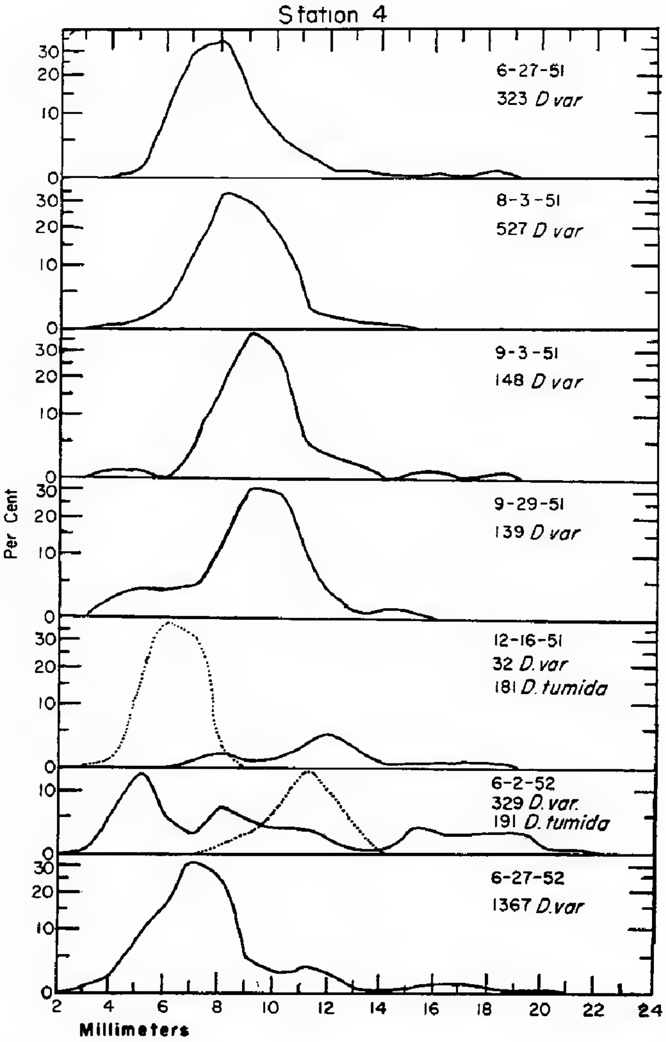

FIG. 10. Length-frequency graphs of *D. variabilis* and *D. tumida* at Station 4.

population along the beach may each play an important part. For example, suppose a population grows one millimeter in the interval between the samplings, but is continually drifting north along the beach. At the subsequent sampling date the clams at a station will have come from some place south. If these clams had been smaller initially, no apparent growth would be indicated on the length-frequency graph even though growth occurred. The length-frequency curves can indicate growth only if the mortality is the same for all sizes, if the small clams enter the population by an entire size group at a time, and if there is no drift along the beach.

The northern stations generally had a bimodal curve with the peak of the mode of the larger clams at 18 millimeters. This peak at 18 millimeters was progressively weaker at each station, going from north to south, until it disappeared completely at the most southern station, Station 5. Clams of 5 millimeters and less were never numerous at Stations 1 and 2 but were relatively numerous on several occasions from September to June at the other stations. This might indicate that the larvae settled or "set" principally at the southern stations, or it might indicate that sets of the same density at the northern stations were greatly outnumbered by the larger clams that may have drifted up from the south.

The clams seemed to grow faster in fall and winter than in summer, with an apparent sudden increase in growth in October. The apparent rate of growth was more rapid at the northern stations. The mode of the smaller clams at Station 1 advanced from 9 millimeters to 16 millimeters in the four months from June 27 to October 27, for an average advance of 1.75 millimeters per month. During this same period of time the advance of the clams at Station 3 was only 0.67 millimeter per month and at Station 5 only 0.33 millimeter per month.

No obviously new set of *Donax* was ever observed, but the clams 3 to 4 millimeters long have very thin, light, and fragile shells and have probably not been out of the plankton very long. These were most numerous in September.

At least one group of *Donax* with a mode at about 12 millimeters in December overwinters on the Texas coast. They are found in the edge of the water in winter, and in deeper water after northers. The deepest water examined in the winter was as deep as a pair of hip boots would permit. It is possible that more than one size group lives over the winter. On June 2, 1952 most of the stations showed three peaks in class frequencies. Apparently those *Donax* that reached 18 millimeters early in the summer were those which weathered the previous winter. When a strong mode of 18 millimeters was reached there seemed to be little growth and only once was a modal strength of 19 millimeters reached.

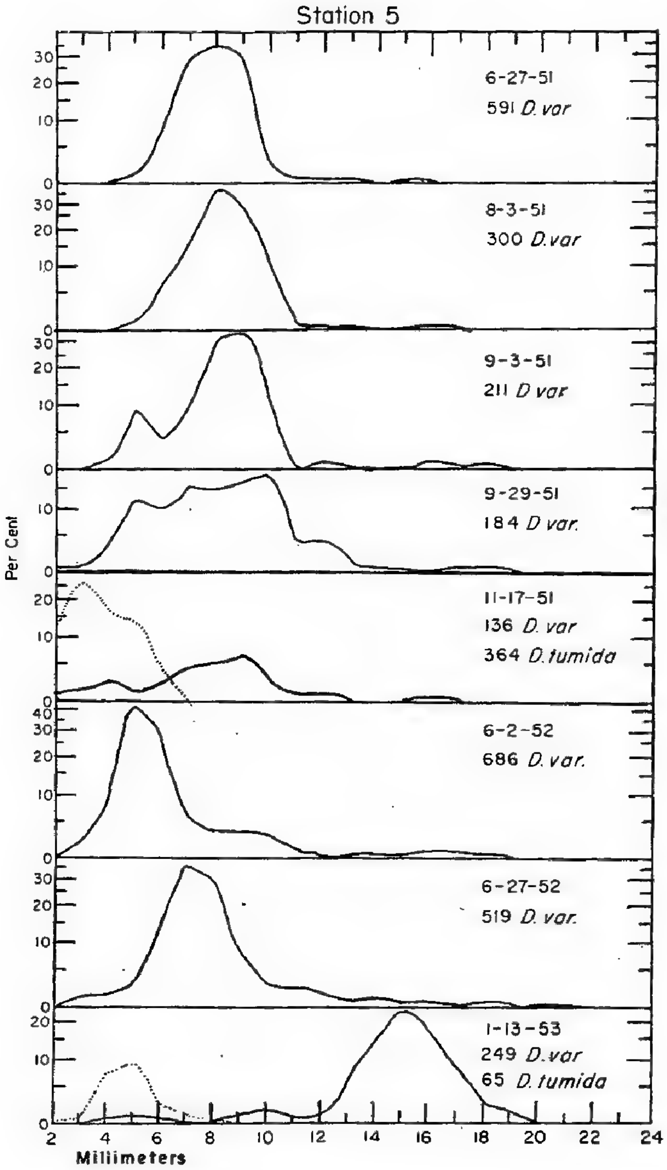

FIG. 11. Length-frequency graphs of *D. variabilis* and *D. tumida* at Station 5.

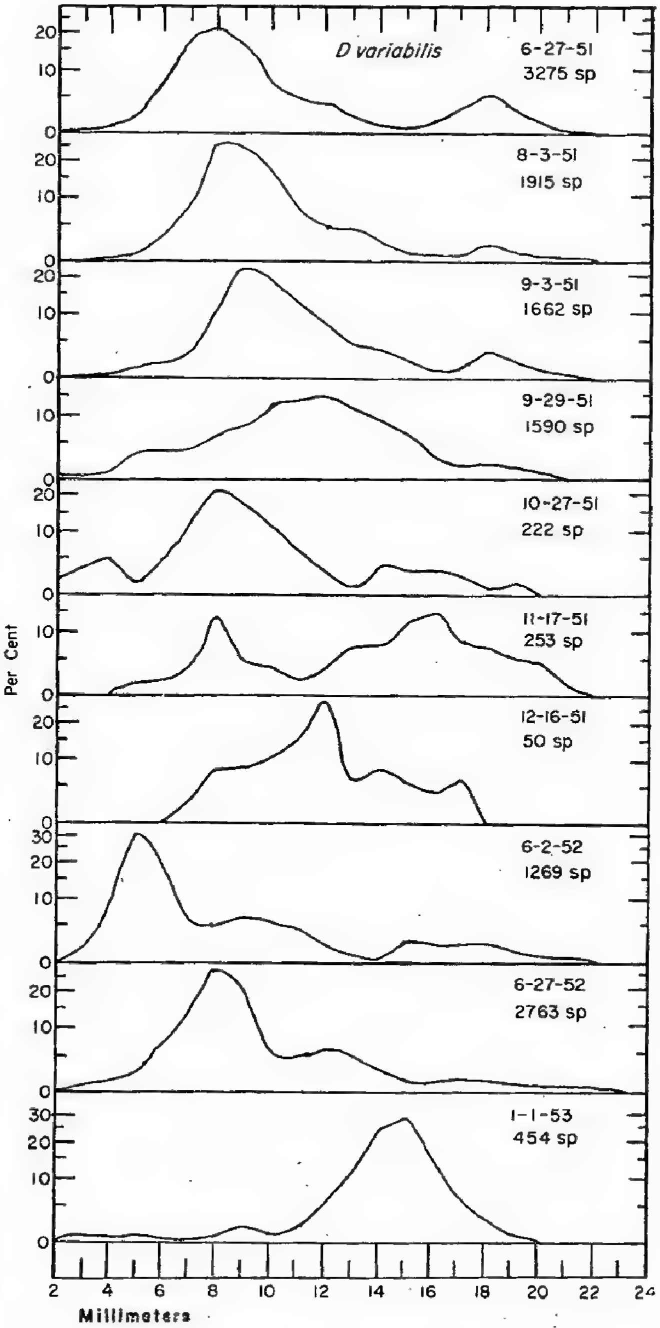

FIG. 12. Composite length-frequency graphs of *D. variabilis* at all stations.

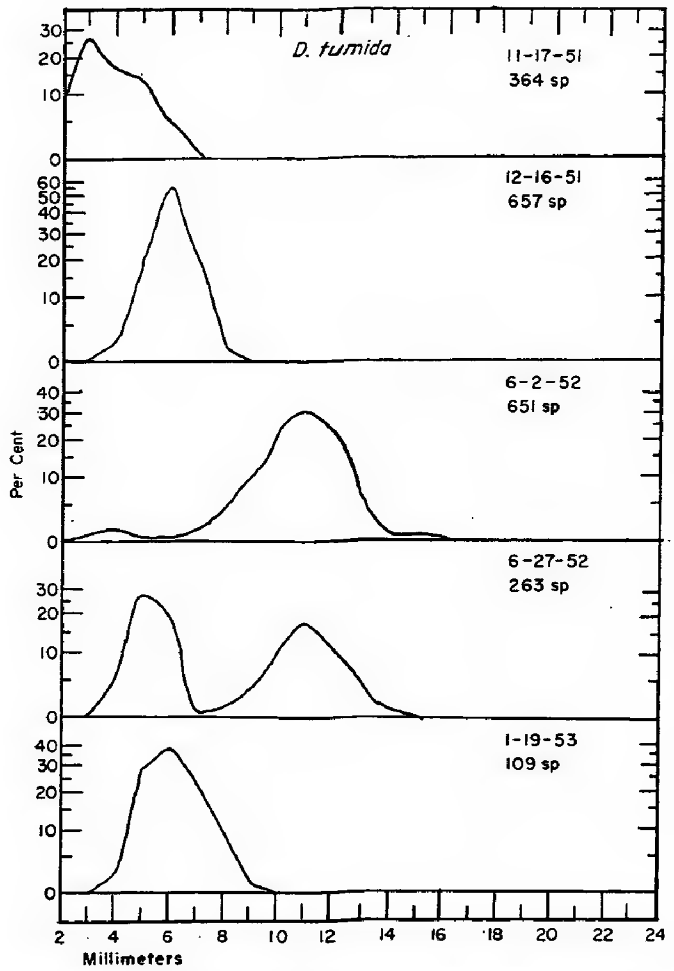

FIG. 13. Composite length-frequency graphs of *D. tumida* at all stations.

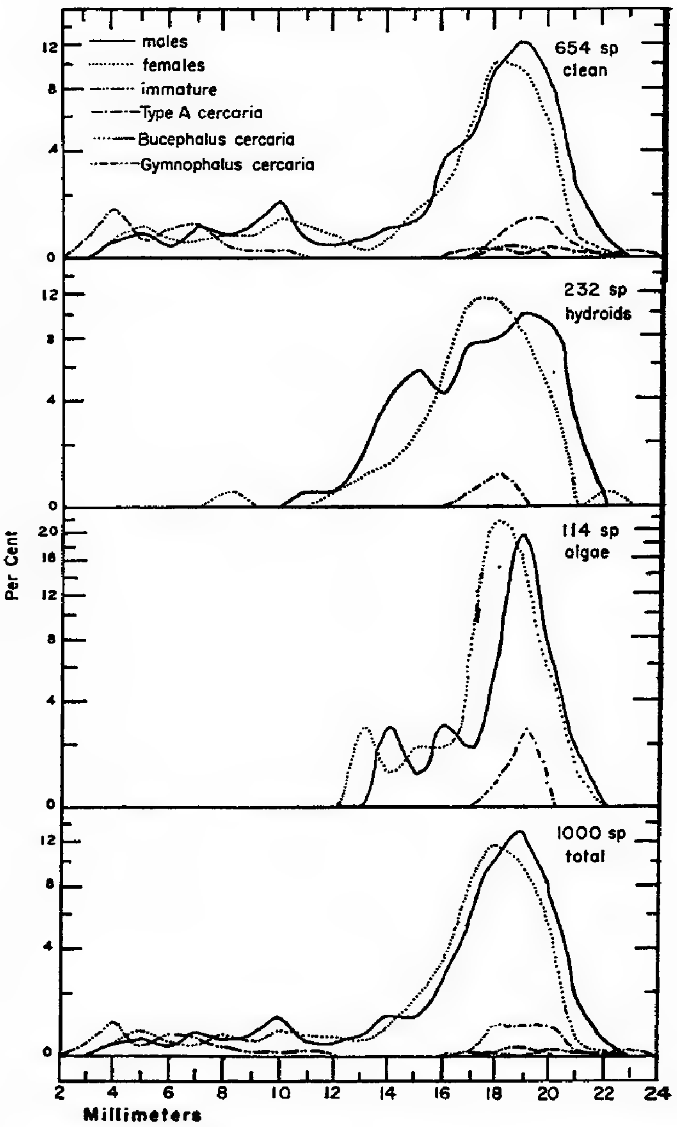

FIG. 14. Length-frequency graphs of *D. variabilis* showing males, females, immature clams, and clams infested with "A" type cercariae, *Bucephalus* cercariae and *Gymnophallus* cercariae.

Apparently, a die-off of *D. variabilis* occurs in late September and early October. The mode of 16 to 18 millimeter clams faded at this time; these clams probably died, for a great decrease in population occurred at this time along with an increase of hinged shells on the beach.

DONAX TUMIDA

From June 1951 to November 1951 no *D. tumida* were found in the same population with *D. variabilis.* Samples were taken only at Stations 1 and 5 on November 17, 1951, and at Station 5 both species were found. In this sample the mode of *D. variabilis* was 9 millimeters and the mode of *D. tumida* was 3 millimeters. Then on December 16, 1951 more than half of all clams taken at each station were *D. tumida.* Some *D. tumida* were taken in each subsequent sample. All earlier samples have been rechecked and no sample taken prior to November 17, 1951 contained *D. tumida.*

On June 27, 1952 the percentage of *D. tumida* decreased greatly from that of June 2 of the same year. It is possible that many *D. tumida* die at this time. Such mortality might explain the absence of *D. tumida* in the June 1951 to November 1951 samples.

Unfortunately there is a gap in the sampling dates from December 1951 to June 1952. Had monthly samples been taken during this period a much clearer picture could be had. From the meagre data available, it appears that the apparent growth of *D. tumida* is approximately 1 millimeter a month. At Station 1 the mode of these clams advanced from 6 millimeters in December 1951 to 12 millimeters in June 1952; and at Station 4 the mode advanced from 6 to 11 millimeters during the same period. The largest *D. tumida* found was 15 millimeters long as compared to 22 millimeters for *D. variabilis.*

Sex Ratios and Parasites

During the course of this investigation, 1000 *D. variabilis* were sexed, examined for parasites, and measured in three different groups: (1) those with a growth of algae on the shells, (2) those with a growth of hydroids on their shells, and (3) those with neither algae nor hydroids on their shells.

Nearly all of this sexing, measuring, and examining for parasites was done with fresh material. Some material collected during the summer preceding the major part of the study had been preserved and was examined after preservation. Some was preserved and examined later. Figure 14 is a graphic illustration of these data.

In addition to the cercarial and precercarial parasites metacercariae were found encysted in all of the *Donax* examined. These metacercariae were of two types, one a *Gymnophallus* type that was usually found in the umbo region between the mantle and the shell, and the other a more advanced stage of the "A" type cercaria shown in Figure 16 that was encysted in the rest of the clam and particularly around the siphon tubes and foot.

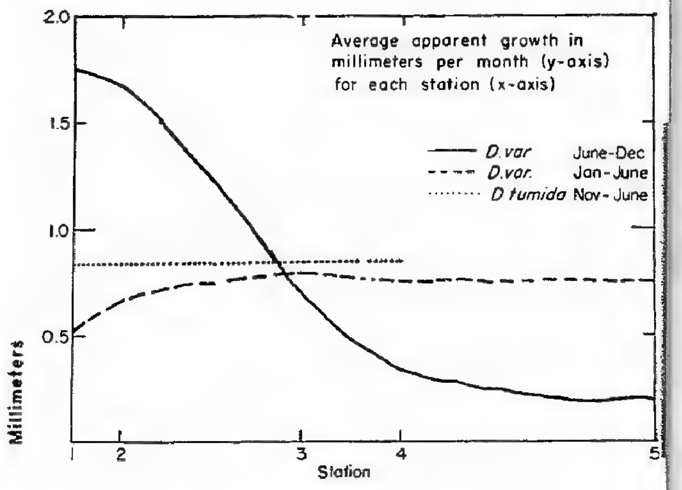

FIG. 15. Average apparent growth in millimeters per month (y-axis) for each station (x-axis) for *D. tumida* and *D. variabilis* for two different seasons of the year.

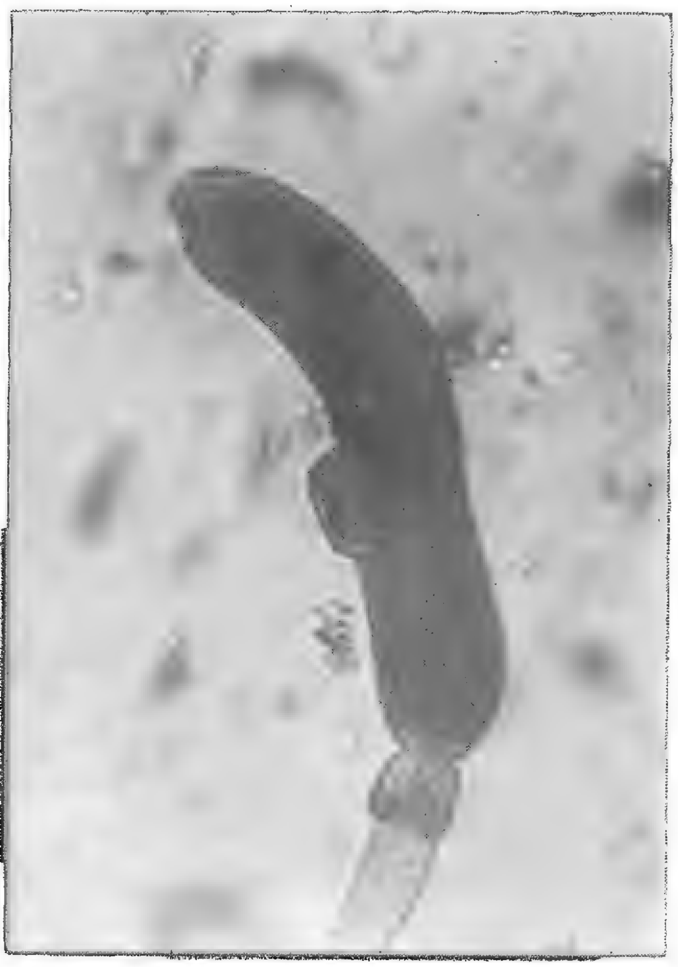

FIG. 16. Photograph of "A" type cercaria ex *D. tumida.*

SEX RATIO

It will be noted that of those *Donax variabilis* 19 millimeters and larger more than half in each size group were males (Table 11), The majority of those 15 to 18 millimeters long were females. Those smaller than 15 millimeters had a few more male than females but not enough more to be statistically significant.

TABLE 11

Males and Females in *D. variabilis*

	Clean		Hydroids		Algae	
Size in mm.	Males	Females	Males	Females	Males	Females
3–14	52	46	6	4	1	0
15–18	108	111	59	73	25	47
19–22	150	115	58	29	39	28
Total	310	272	123	106	65	75

Using these data along with Figure 14 it can be seen that above 18 millimeters most individuals were males in each size class with the exception of one at 22 millimeters. Special attention should be called to the numbers of the 19 to 22 millimeter males in all three groups. There are more males than females in each case. If the males grow at a faster rate than the females, therefore preceding them in the curve, the trend towards the larger males should show up during the entire life and become more pronounced as a larger size is attained. A differential mortality could account for different sex ratios at different sizes, but each of the curves has very nearly the same total number of males as females. A better explanation may be that the males in *Donax* attain a larger size than do the females.

The squares of fifteen subsamples of clean clams, seven subsamples of clams with algae, and two subsamples of clams with hydroids were computed and on the assumption that males and females would be found in a 50–50 ratio. Significant interaction was found in the *Donax* in this sample. Females outnumbered the males in all three samples taken in June, but the males outnumbered the females in the four samples taken in July, August, and September. The explanation is not known. Preserved material was checked later to corroborate these findings.

Thirty-two *D. variabilis*, ranging in size from 3 to 11 millimeters, were found to be so undeveloped sexually that it was impossible to classify them as males or females. The smallest sexually developed males and females of *D. variabilis* were 4 millimeters long. A bar graph showing the percentages of immature clams in each millimeter size group is shown in Figure 17 based on 115 specimens.

Twenty-nine *D. tumida*, ranging in size from 3 to 7 millimeters, were found to be all sexually mature. Of these, 15 were males and 14 were females.

PARASITIC CASTRATION AND ALGAL PROTECTION

Three separate cercarial and precercarial trematode parasites were found in the gonadal region of *D. variabilis*. The percentage of clams infected with precercarial and cercarial parasites for each size interval from 16 to 23 millimeters is shown on Figure 18. When the parasites were present seldom was there any gonadal material left. There were two exceptions, once with each sex, where the "A" type cercaria was found inside sporocysts of what appeared to be relatively new infections. The smallest clam found to

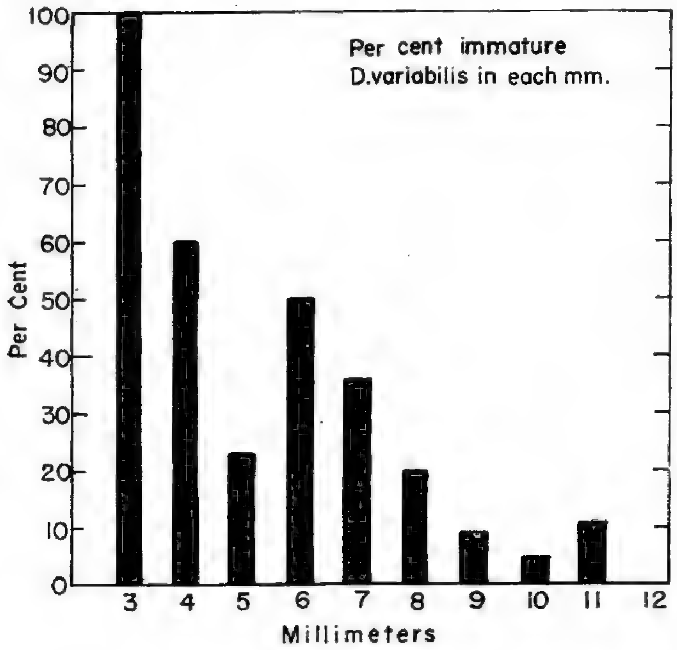

FIG. 17. Bar graph showing the per cent of immature *D. variabilis* in each millimeter size from 3 to 12.

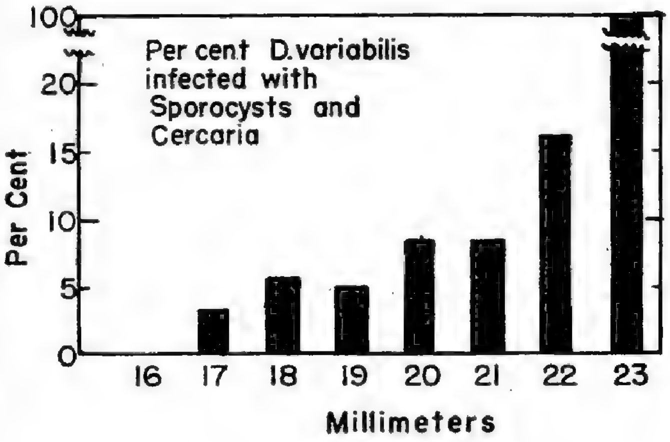

FIG. 18. Bar graph showing the per cent of *D. variabilis* in various size groups infested with sporocysts and cercariae.

have a cercarial or precercarial infection was 17 millimeters long. Fewer parasites were found in hydroid-bearing clams. The difference was significant statistically as indicated by fiducial limits. It may be that the hydroids strain out the miracidia before they enter the incurrent siphon of *Donax,* and may use these trematode larvae for food. Those clams with algae also had a lower proportion of infections than did the clean *Donax.*

Among clams without algae or hydroids, the larger the clam the higher was the incidence of infection. Among those clams with hydroids or algae attached the greatest incidence occurred in the 18 to 19 millimeter individuals.

GYMNOPHALLUS AND *BUCEPHALUS* CERCARIA

Gymnophallus cercariae have in the past been reported as tailless. Dr. Sewell H. Hopkins (personal communication) thinks that the metacercarial stage may have been mistaken for the cercaria after losing its tail. The cercaria seen in *Donax* at Port Aransas will fold its furcocercous tail under the body and rapidly beat the tail in a swimming motion. Cable (1953) reports that *Gymnophallus* generally has a tailless cercaria but suggests that some species probably have a furcocercous cercaria. The type of furcocercous cercaria associated with *Gymnophallus* is known as the dichotoma type after *Cercaria dichotoma* Mueller 1855. Markowski (1936) suggested that the dichotoma group of cercariae were larval stages of *Gymnophallus.* Hopkins's line drawing of this cercaria is shown in Figure 19.

Cable points out that some dichotoma type cercariae lose the tail very easily and quickly, and some may never have a tail. He also stated, as did Hopkins, that some tailless "cercariae" of *Gymnophallus* described in Europe were really metacercariae. The metacercaria is shown in Figure 20 in a line drawing by Hopkins.

Sporocysts containing cercariae were identified by Hopkins as *Bucephalus.* Only three of the *Donax* examined were so infected.

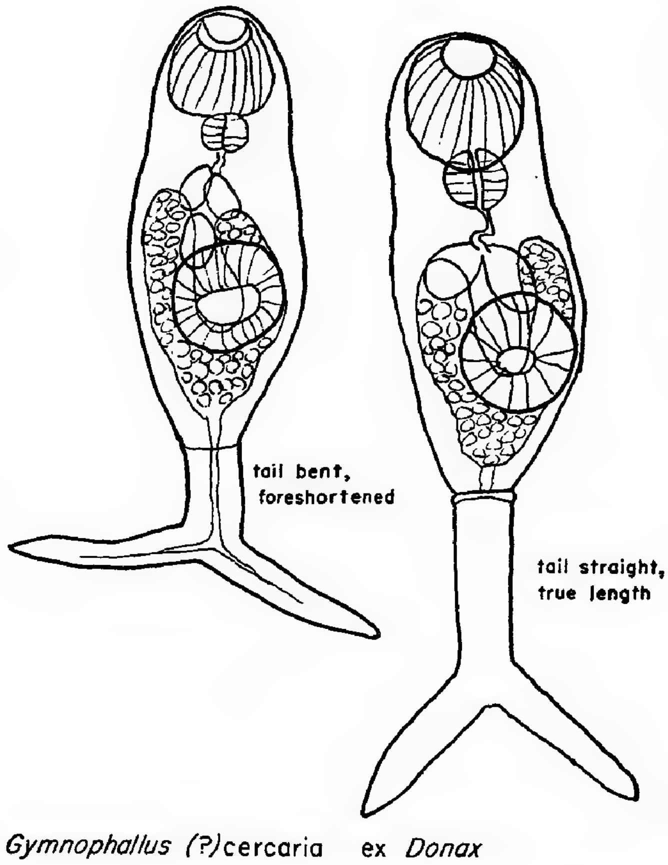
tail bent, foreshortened
tail straight, true length
Gymnophallus (?) cercaria ex *Donax*

FIG. 19. Camera lucida drawing of *Gymnophallus* (?) cercaria ex *D. variabilis.*

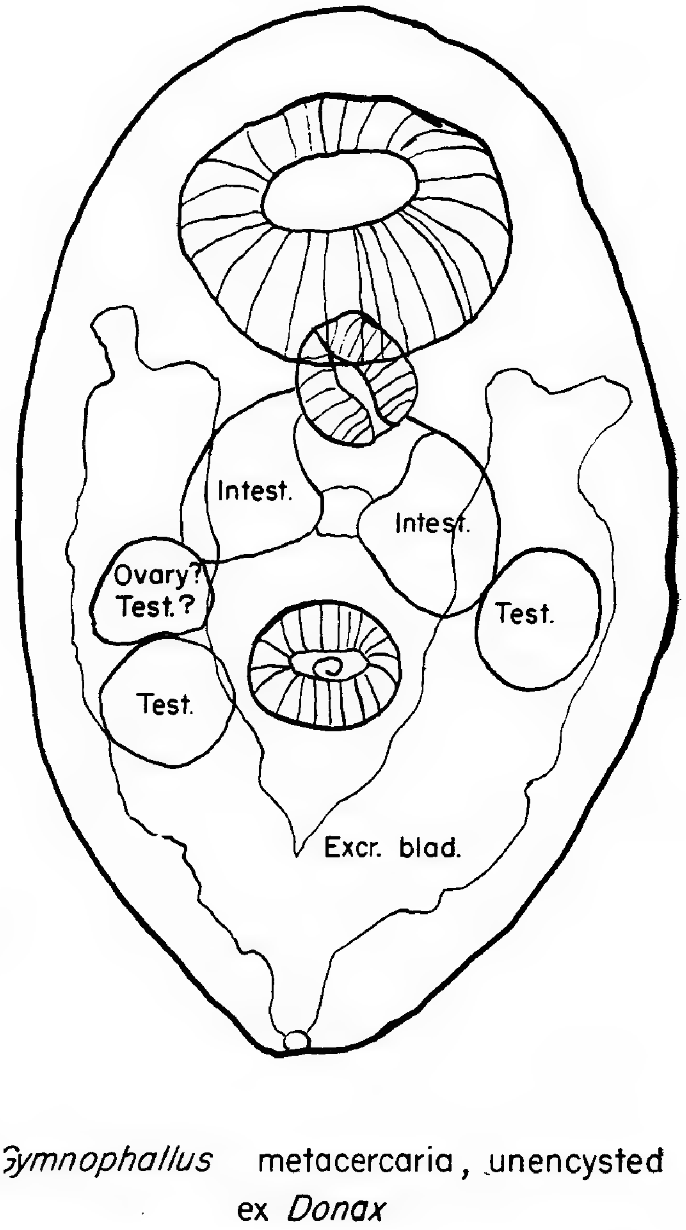
Intest.
Intest.
Ovary?
Test.?
Test.
Test.
Excr. blad.
Gymnophallus metacercaria, unencysted ex *Donax*

FIG. 20. Camera lucida drawing of *Gymnophallus* metacercaria ex *D. variabilis.*

"A" TYPE CERCARIA

For want of a better name, the most common cercaria found was called the "A" type cercaria. It was distinguished by possession of a highly specialized tail of unique type. A photograph of this worm is presented in Figure 16.

The opecoelids have a cup-like or cotylocercous tail similar to that found in this cercaria. However, there is a rudimentary tail projecting from the cup on the "A" cercaria. When Hopkins sent a sketch to R. M. Cable, Cable replied that the cercaria was a monorchid and not an opecoelid. "It develops in a Lamellibranch, it has a spinose cuticle, it lacks a stylet in the oral sucker, and while the tail has a cup-like portion as in opoecilids, there projects from the cup a short appendage with lappets along the edges; the structure of this appendage is precisely that of the entire tail in monorchid cercariae with well developed tails. All of these characters are non-opecoelid."

OTHER PARASITES, METACERCARIAE

One female *Donax* had an immature trematode of the family Aspidogastridae. This worm belonged to one of the two species of *Lobatostoma*, according to Hopkins.

Metacercariae. Particular emphasis was placed on the examination for castrating cercariae and precercariae, and very little on metacercariae. In early June 1951 eight *D. variabilis* ranging in size from 8 to 20 millimeters were examined and all contained "A" type metacercariae. In late June 1951 eleven clams ranging in size from 6 to 19 millimeters were examined for *Gymnophallus* metacercariae and all contained them. No other records were kept of these metacercariae but they were noted in nearly all the clams, so it can be assumed that at least 90 per cent and probably 100 per cent of the clams had these parasites.

All *D. tumida* examined from Grand Isle, Louisiana, were infected with "A" type metacercariae. A large but unknown number of the *Donax* of both species examined at Port Aransas harbored the metacercariae of the "A" type.

Tissue of both *D. variabilis* and *D. tumida* were cultured in the thioglycollate technique as specified by Ray for Dermocystidium. About thirty moribund *D. tumida* from Grand Isle and apparently normal *D. variabilis* from Texas were found to be negative. Mackin (personal communication) has checked a number of *Donax* from Grand Isle, Louisiana, and Port Aransas, Texas, by sectioning and culturing and has found no *Dermocystidium* in the clams. Mackin suggests, however, that it is possible that all species of *Dermocystidium* do not respond to the thioglycollate technique. It is also possible that some of the lower Chytrids may produce hypnospores by thioglycollation.

Coe (1955) mentions finding irregularly spherical or ovoid cells 2 to 6μ in diameter in moribund *Donax* which appeared to be similar to *Dermocystidium marinum.* Although *D. marinum* is a larger organism, it is possible that the California species is related.

Summary

1. An ecological study of two species of *Donax* was made at Mustang Island, Texas, during the summer of 1951. Natural history, populations, predators, parasites, systematics, growth, and sex ratios were studied.
2. Two species of *Donax, D. variabilis roemeri* and *D. tumida,* were found at Mustang Island, Texas. These species were mixed in the winter and spring, but during the summer *D. variabilis* were found at the edge of the water and *D. tumida* were found in water three feet deep. A number of physical differences in the two species were noted.
3. *Donax variabilis* has an adaptive behavior that allows it to live in the surf-pounded beach. During the rising tide the clam is stimulated through the sand by the vibration from a breaking wave. The clam then pushes its way to the top of the sand and allows the wave to carry it higher on the beach where it immediately buries itself. With a falling tide the clams rise after the water passes over the population and are carried down with the retreating wave. They lie exposed on the beach at the interval of tide change. Experiments indicate that the surf-pounded beach is necessary for survival and growth.
4. The greatest number of *Donax* was found in June, with a gradual decrease towards fall. In winter the clams were in deeper water and so the number could not be estimated.
5. Three different larval trematode parasites were found in *D. variabilis.* When the cercarial or precercarial stage was present, only rarely was there any gonadal material in the clam. All cercarial and precercarial parasites were found in clams 17 millimeters long or larger. Metacercariae of two of these parasites were found in *D. variabilis.* There

was a 100 per cent infestation by metacercariae of one species ("A" type) and a high rate of infestation of *Gymnophallus* metacercariae. The "A" type metacercariae were also found in *D. tumida.*

6. Clams with commensal hydroids and algae were less infected with parasites than clean clams.

7. Birds and fish were observed to feed on *Donax* but the adult stage of these trematode parasites was not found in some potential hosts examined.

8. Length-frequency charts prepared at approximately monthly intervals showed an average monthly increase in length of *D. variabilis* ranging from 0.25 millimeter at the southernmost stations on Mustang Island to 1.75 milimeters at the most northerly station during the period from June to December. From January to June there was an apparent increase of about 0.75 millimeter per month. No increase in modal size was observed in clams of the 18 millimeter mode.

9. It seems probable that these clams live only a year. Apparently *Donax variabilis* at Mustang Island overwinters at 8 to 12 millimeters, during the summer increases to 18 millimeters, and then disappears in August or September. Most of the older individuals of *D. tumida* apparently die off in May and June.

LITERATURE CITED

Cable, R. M. 1952. Studies on marine digenetic trematodes of Puerto Rico. The systematic position of the subfamily Gymnophallinae Odhner. *J. Parasit.*, 38 (No. 4, Sec. 2): 36–37. (Abstract).

————. 1953. The life cycle of *Parvatrema borinquenae* gen. et sp. nov. (Trematoda: Digenea) and the systematic position of the subfamily Gymnophallinae. *J. Parasit.*, 39 (No. 4, Sec. 1): 408–421.

Chatton, E., and A. Lwoff. 1923. Un cas remarquable d'adaption: *Ellobiophyra donacis* n. g., n. sp., péritriche inquilin des branchies de *Donax vittatus. C. R. Soc. Biol.*, Paris, 88: 749–752.

Coe, W. R. 1946. A resurgent population of the California bay mussel *(Mytilus edulis diegensis) J. Morph.*, 78 (1): 85–103.

————. 1953. Resurgent populations of littoral marine invertebrates and their dependence on ocean currents and tidal currents. *Ecology*, 34 (1): 225–229.

————. 1955. Ecology of the bean clam *Donax gouldi* on the coast of southern California. *Ecology*, 36: 512–513.

Cole, H. A. 1935. On some larval trematode parasites of the mussel *(Mytilus edulis)* and the cockle *(Cardium edule).* Part II. A new larval *Gymnophallus (Cercaria cambrensis)* sp. nov. from the cockle. *Parasitology*, 30: 40–43.

Cole, H. A. 1938. On some larval trematode parasites of the mussel *(Mytilus edulis)* and the cockle *(Cardium edule).* Part II. A new larval *Gymnophallus (Cercaria cambrensis)* sp. nov. from the cockle. *Parasitology*, 30: 40–43.

Dall, W. H. 1892. On the species of *Donax* of eastern North America. *Nautilus*, 5: 125–127.

————. 1921. Summary of the marine shellbearing mollusks of the northwest coast of America from San Diego, California, to the Polar Sea, mostly contained in the collection of the United States National Museum, with illustrations of hitherto unfigured species. *Bull. U.S. Nat. Mus.*, 112: 1–217.

Giard, A. 1897a. Sur un cercarie setigere *(Cercaria lutea)* parasite des pelecypodes. *C. R. Soc. Biol.*, Paris, 49: 954–956.

————. 1897b. Sur un distome *(Brachycoelium sp.)* parasite des pelecypodes. *C. R. Soc. Biol.*, Paris, 49: 956–957.

————. 1907. Sur les trematodes margaritigenes du Pas-de-Calaise. *C. R. Soc. Biol.*, Paris, 63: 416–420.

Graham, Alastair. 1934a. The cruciform muscle of Lamellibranchs. *Proc. Roy. Soc. Edinb.*, 54 (1): 17–30.

————. 1934b. The structure and relationships of Lamellibranchs possessing a cruciform muscle. *Proc. Roy. Soc. Edinb.*, 54 (2): 158–187.

Haas, Fritz. 1940. Ecological observations on the common mollusks of Sanibel Island, Fla. *Amer. Mid. Nat.*, 24 (2): 369–378.

Harry, Harold W. 1942. List of mollusca of Grand Isle, Louisiana, recorded from the Louisiana State University Marine Laboratory 1929–41. *Occ. Pap. of the Mar. Lab. La. Univ.*, 1: 1–13.

Hutton, Robert F. 1952. Studies on the parasites of *Cardium edule* L.: *Cercaria fulbrighti* n. sp., a *Gymnophallus* larva with a forked tail. *J. Mar. Biol. Ass. U. K.*, 31 (2) : 317–326.

————. 1953. *Cercaria reesi* n. sp., a new furcocercous larvae from Plymouth. *J. Mar. Biol. Ass. U. K.*, 31 (3) : 581–585.

Ihering, H. von. 1900. The musculus cruciformis of the order Tellinacea. *Proc. Acad. Nat. Sci., Phil.*, 52: 480–481.

Jacot, Arthur. 1922. Review of marine mollusca found about New York City. *Nautilus*, 36: 59–61.

Jacot, Arthur. 1929. Range of *Donax variabilis. Nautilus*, 42 (4) : 142–143.

Jameson, H. L., and W. Nicoll. 1913. On some parasites of the scoter duck *(Oidemia nigra)* and their relation to the pearl-inducing trematode in the edible mussel *(Mytilus edulis). Proc. Zool. Soc.*, London, 12: 53–63.

Johnson, Charles W. 1927. *Donax fossor*, not *D. variabilis. Nautilus*, 41 (1) : 140.

————. 1929. Further notes on *Donax fossor* and *Donax variabilis* Say. *Nautilus*, 43: 29–30.

————. 1934. List of marine mollusca of the Atlantic coast from Labrador to Texas. *Proc. Boston. Soc. Nat. Hist.*, 40: 1–204.

Kudo, R. R. 1947. Protozoology. 3rd edition, Springfield, Ill., Charles C. Thomas, pp. 1–778.

Leidy, Jos. 1879. Entozoa of *Donax fossor. Proc. Acad. Nat. Sci.*, Phil., 30: 382–383.

MacGinitie, G. E., and Nettie MacGinitie. 1949. Natural History of Marine Animals. New York, McGraw-Hill Book Co., pp. 1–473.

Markowski, St. 1936. Ueber die Trematodenfauna der baltischen Mollusken aus der Umgebung der Halbinsel Hel. Bull. Acad. Polonaise Sci. Lett., Ser. B, 2: 285–317.

Miner, Roy Waldo. 1950. Field Book of Seashore Life. New York, G. P. Putnam's Sons, pp. 1–888.

Mori, Synuiti. 1938. Characteristic tidal rhythmic migration of a mussel, *Donax semignosus* Dunker, and the experimental analysis of its behavior at flood tide. *Zoological Magazine* (Japan), 50 (1) : 1–2.

————. 1950. Characteristic tidal rhythmic migration of a mussel, *Donax semignosus* Dunker, and the experimental analysis of its behavior. *Zool. Mag.*, Tokyo, 59 (4) : 87–89.

Odhner, T. 1905. Die trematoden des arktischen Gebietes. *Fauna Arct.*, Jena, 4 (2) : 291–372.

Orton, J. H. 1929. Severe environmental mortality among *Abra (Syndosmya) alba, Donax vittatus*, and other organisms off the Lancashire coast. *Nature*, London, 124: 911.

Palombi, A. 1924. Le cercarie del genere *Gymnophallus* Odhner dei mitili. *Publ. Staz. Zool. Napoli.*, 5: 137–152.

Pearse, A. S., H. J. Humm and G. W. Wharton. 1942. Ecology of sand beaches at Beaufort, North Carolina. *Ecol. Monogr.*, 12: 137–190.

Pelseneer, Paul. 1896. Un trematode produisant la castration parasitaire chez *Donax trunculus. Bull. Sci. Fr. Belg.*, 6: 357–363.

————. 1928. Les parasites des mollusques et les mollusques parasites. *Bull. Soc. Zool. Fr.*, 53: 158–189.

Pilsbry, Henry A. 1919. Mollusca from Central America and Mexico. *Proc. Acad. Nat. Sci.*, Phil., 71: 212–223.

Pilsbry, Henry A., and H. N. Lowe. 1932. West Mexican and Central American mollusks collected by H. N. Lowe, 1929–31. *Proc. Acad. Nat. Sci.*, Phil., 84: 33–144.

Pulley, T. E. 1952. An illustrated check list of the marine mollusks of Texas. *Tex. J. Sci.*, 4 (2) : 167–199.

Ray, Sammy M. 1952. A culture technique for the diagnosis of infections with *Dermocystidium marinum* Mackin, Owen, and Collier in oysters. *Science*, 116 (3014) : 360.

Rees, F. G. 1939. *Cercaria strigata* Lebour from *Cardium edule* and *Tellina tenuis. Parasit.*, 31: 458–463.

Reish, D. J. 1950. New host and distribution records for two trematodes from the western gull. *J. Parasit.*, 36: 84.

Snedecor, George W. 1946. Statistical Methods. Ames, Iowa, Iowa State College Press.

Strong, A. M. 1924. Notes on the *Donax* of California. *Nautilus*, 37: 81–84.

Talavera, F., and L. A. Faustino. 1933. Edible mollusks of Manila. *Philipp. J. Sci.*, 50: 1–48.

Tomlin, J. R. 1926. Note on *Donax conradi* Deshayes. *Nautilus*, 40 (2) : 52–53.

Uzmann, Joseph R. 1952. *Cercaria myae* sp. nov. a fork-tailed larva from the marine bivalve, *Mya arenaria. J. Parasit.*, 38 (2) : 161–164.

Vanatta, E. G. 1904. A list of shells collected in western Florida and Horn Island, Mississippi. *Proc. Acad. Nat. Sci.*, Phil., 55: 756–759.

Williamson, M. B. 1892. An annotated list of the shells of San Pedro Bay and vicinity. *Proc. U.S. Nat. Mus.*, 15: 179–220.

Wood, Albert Elmer and Horace Elmer Wood, 2nd. 1927. A quantitative study of the marine mollusks of Cape May County, New Jersey, *Nautilus*, 41: 8–18.

The Summer Marine Flora of Mississippi Sound

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Introduction

That the marine algae of the coastal waters of Mississippi are virtually unknown is indicated by Taylor (1954), who lists but eight species in a paper on the distribution of marine algae in the Gulf of Mexico. Those listed represent a collection made in December, 1948, by Dr. Francis Drouet primarily from the intertidal zone of the mainland side of Mississippi Sound between Ocean Springs and Bay St. Louis.

While associated with the summer sessions of 1954 and 1955 at the Gulf Coast Research Laboratory, Ocean Springs, Mississippi, the authors had an opportunity to collect the marine algae of Mississippi Sound at several stations along the inner shore of Ship Island; from Ship Island Pass at the western end of the island; and from several other localities. As a result of these collections 77 species of marine and brackish water algae have been determined as comprising the principal summer flora of Mississippi Sound.

We hereby express our appreciation to Mr. E. V. Richards of Gulf Hills, Ocean Springs, for the use of his diving equipment; and to Capt. L. L. Arbon of the United States Air Force for locating for us a submerged wreck off the sound side of Ship Island.

THE HABITAT

Collecting Stations. The northern and western sides of Fort Massachusetts, located near the western end of Ship Island are washed by the waters of Mississippi Sound, even at low tide. In addition to the fort wall itself, there is a fringe of large rocks most of which are submerged. These serve to mitigate the action of the surf against the fort wall.

About 100 feet north of the fort and extending for over 100 feet in an east-west direction is a sunken iron barge, the top of which is awash at low tide. The sides of the barge are four to five feet high.

Adjacent to the fort and running northward into the sound is a pier of 300 feet or more in length, supported by wooden pilings. To the northeast of the fort is a T-shaped rock breakwater, most of which is submerged at all stages of the tide. Beyond the breakwater, both east and northeast, in three to six feet of water are rock piles of discarded ballast from old sailing vessels, part of an old brick cistern, and the completely rusted boiler of a small steam vessel. About two-fifths of a mile northeast of the fort is the Ship Island lighthouse where there are extensive breakwaters and another large, wooden pier. About one mile northeast of the light and at least three-quarters of a mile offshore in 10–12 feet of water is the rusted ironwork remains of what is said to be a ship that was sunk during the Civil War. A tangle of rusted cable, chain, and pipes extends about four feet above the bottom. Much of this is covered with unusually large living oysters and empty shells.

About three miles east of the lighthouse and fort, also on Ship Island, is the former quarantine station, now an Air Force recreational area. There is a wooden pier about 1000 feet long that extends north into the sound. About one-half mile northeast of the pier are extensive areas of ballast rock in low piles in six to ten feet of water.

In Ship Island Pass, at the western end of the island, is a ship channel which extends from Gulfport several miles southward into the Gulf itself. The channel is marked by nun and lighted buoys which are left undisturbed about a year before they are relieved, cleaned and painted.

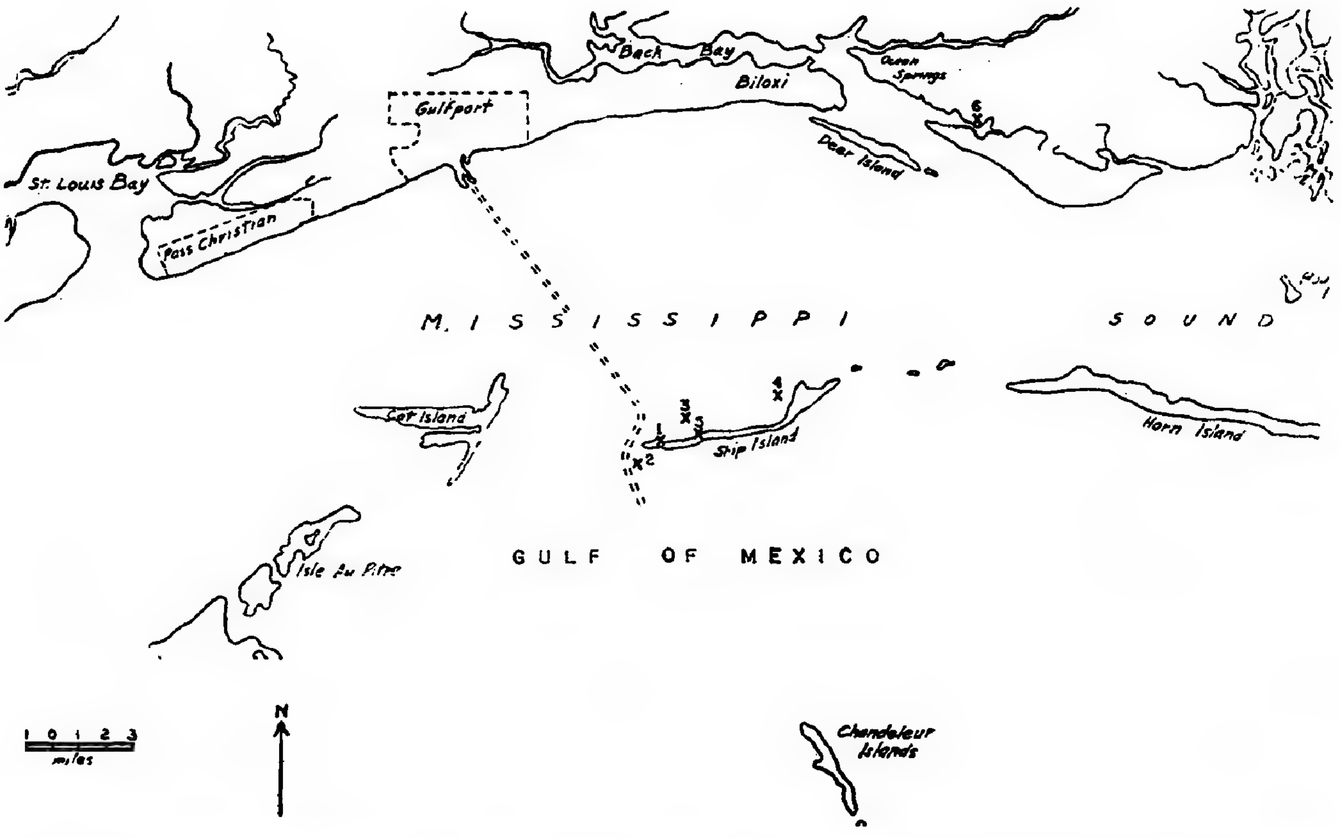

FIG. 1. Map of Mississippi Sound showing adjacent mainland and barrier islands. The principal collecting stations and the Gulf Coast Research Laboratory are located by an X and numbered as follows: 1. Fort Massachusetts, Ship Island. 2. Ship Island Pass channel buoys. 3. Submerged wreck. 4. Ballast rocks in 10–15 feet of water off the former quarantine station. 5. Ship Island lighthouse. 6. Gulf Coast Research Laboratory located just east of Ocean Springs.

Figure 1 shows the general area and locates by number the principal collecting stations.

Temperature and Salinity. Water temperatures of Mississippi Sound generally range from about 28° to 30° C. between June 1 and September 1. Even higher temperatures may be recorded in very shallow water or in tide pools, and slightly lower temperatures may occur along the bottom in depths exceeding five or six feet. There is considerable stratification even in shallow water so that it is difficult to present precise temperature data.

The salinity of the waters along the sound side of Ship Island generally ranges from about 20 to 32‰. After rainy periods, dilution of sea water with as much as one-third fresh water may be observed at this distance from the mainland, but there are times when the salinity of the outer beach water exceeds 30‰. Because of the irregular fluctuations in salinity there are marked fluctuations in the algal flora at these stations each summer. After two weeks or more of relatively high salinity, species may appear which are able to persist only while the salinity is elevated. These quickly disappear following sudden drops in salinity to points below 25‰. Records of surface water salinities, however, are not necessarily representative of the salinity of the water surrounding algae located a few feet below low tide. During the summer of 1955, apparently a typical year, salinity records ranged from 21 to 32‰ in the vicinity of Fort Massachusetts.

Light Penetration. Water transparency, as would be expected, also fluctuates widely at these stations. While specific photometer or Secchi disk data were not obtained, a general idea of transparency can be gained from the observations that under poorest conditions the bottom was visible at a maximum depth of about three feet, while under best conditions, bottom could be seen along the sound side of Ship Island at six feet depth.

Tidal Effects. The mean tidal range in Mississippi Sound is 1.9 feet and tides are diurnal rather than semidiurnal. Currents are weak, are almost entirely of tidal origin, and form an increasing gradient in rate from the center of the island toward the ends of the island. Strongest currents occur in Ship Island Pass around the buoys where they may reach one to three miles per hour. Below-mean-low tides occur during the daytime only at approximately eight-day intervals. A below-mean-low tide during the heat of the day results in considerable kill of sensitive species of marine algae that have colonized the intertidal zone during the period of time when daytime low tides were relatively high. Unusually low tides at night apparently do little harm unless a hard rain occurs simultaneously. This alternate recolonization and retreat in the intertidal zone is of more frequent occurrence where tides are diurnal than at stations in other parts of the world where semidiurnal tides prevail. With diurnal tides, there is more time for colonization or growth in height before an extreme low tide occurs.

COLLECTING METHODS

For the most part, collecting was done at low tide by wading or by use of a face mask which permitted underwater observations. Collecting on the submerged wreck and from the ballast rocks off the quarantine station was done by means of diving equipment, usually from the laboratory vessel *Hermes*. Samples were obtained from Ship Island Pass channel buoys by scraping them and by going under with a face mask to obtain material 2 to 6 feet below the surface.

Affinities of the Flora

Among the *Chlorophyta, Phaeophyta,* and *Rhodophyta* listed, the majority in each case show a distribution from New England to Florida and the Gulf of Mexico. These are algae that must be regarded as eurythermal, if species among the algae can be based entirely upon morphological characters, as has always been done. Of the 13 species of green algae listed, 10 occur in New England and 3 are not known north of Cape Hatteras; of the browns, 6 are New England species, and 5 are evidently restricted to the southeastern coast; of the red algae, 14 are found in New England, 10 are southern. On the basis of these distributions, it may be said that the majority of the algae of Mississippi Sound, even during the summer months, show greater affinities with the New England flora than with that of the tropics.

Most of these species which occur in New England are distributed continuously southward along the coast, around the Florida peninsula, and northward along the Gulf coast. There are some, however, which are known only part of the way down the Atlantic coast, seem to be absent around southern Florida, and then occur along the northern Gulf coast between Tampa Bay and Port Aransas, Texas. This interrupted distribution, if it is actually the case and not a result of inadequate collecting, can be explained in several ways.

If it is assumed that year-around water temperatures are too high for these species which do not occur around southern Florida, then the distribution may have been continuous at some time in the past and become discontinuous with rising sea water temperatures since the Pleistocene epoch, resulting in the isolation of certain species along the northern Gulf coast. Such isolation would probably occur only in shallow, inshore waters in which there is a wide range of temperature with season.

An alternative explanation would postulate a continuous distribution along the southeastern coast during the Pleistocene when most of Florida was submerged and the waters of the northern Gulf were continuous with the Atlantic ocean across northern Florida and southern Georgia. Sea water temperatures were considerably lower at this time. Under these circumstances, a number of species not adapted to southern Florida waters may have become established in the northern Gulf, only to be isolated when sea level fell and the Florida peninsula became connected with the continent. This hypothesis is supported by the fact that all species present in the northern Gulf which are not continuous around Florida are also euryhaline. Salinity of the sea was significantly lower during Pleistocene times than at present. Environmental factors other than sea water temperature are probably involved in the distribution of marine algae around the Florida peninsula.

A third, and perhaps less likely explanation, is the assumption that some of the discontinuous species became established in the northern Gulf as a result of transportation on ship bottoms or in ballast tanks in relatively recent times.

The Sea Grasses

Since a separate report has been prepared on the "sea grasses" or marine monocotyledonous plants of the northern Gulf coast with special reference to Mississippi Sound (Humm, 1957), they will merely be mentioned here.

Five species of sea grasses occur in abundance in Mississippi Sound. *Ruppia maritima* L. is common along the mainland shore, especially in bayous where the salinity is usually less than half that of inshore Gulf waters. Although not collected along the sound side of

Ship Island, it may be expected where creeks or springs enter the sound from the island. Extensive beds of *Thalassia testudinum* König, *Cymodocea manatorum* Ascherson, and *Halophila engelmannii* Ascherson occur as a mixture along the sound side of Ship Island and in other islands in the sound. *Thalassia* is usually the most abundant and *Halophila* least abundant. *Diplanthera wrightii* (Ascherson) Ascherson occurs more or less as separate beds and usually nearer the beach than the mixed beds of the other three. All of these plants bear a variety of algae as epiphytes upon the upper ends of the leaves, especially the genera *Fosliella, Achrochaetium, Ectocarpus,* and *Hypnea.*

The Marine Algae

CYANOPHYTA

The majority of the bluegreen algae listed here were collected originally along the mainland side of Mississippi Sound by Drs. Francis Drouet and R. L. Caylor in December, 1948, and can be recognized by the mainland collecting stations given. Most of them were collected again in connection with the present work, indicated by the Ship Island collecting stations cited.

All species of bluegreens listed below were determined by Dr. Drouet except *Anacystis aeruginosa* and *A. marina.*

ORDER CHROOCOCCALES

Family Chroococcaceae

Anacystis aeruginosa (Zanardini) Drouet and Daily (Plate 1, Fig. 1)

Plants pale bluegreen, rose, violet, or with little color, at first microscopic later becoming bullose to several cm. in diameter. Cells spherical or subspherical before division, with adjacent faces flattened after division, 6–12 microns in diameter, distributed in the sheath without order. Sheath hyaline, homogeneous or sometimes indistinctly lamellose delimited or diffluent. Protoplast pale bluegreen, rose, or violet, homogeneous or slightly granular.

On *Gelidium crinale* and other algae from sides of a sunken iron barge near Fort Massachusetts, Ship Island. Forming small clumps of spherical cells mostly 7–10 microns in diameter.

Reference: Drouet and Daily, 1956, p. 76.

Anacystis dimidiata (Kützing) Drouet and Daily (Plate 1, Figs. 2 and 3)

Plants bluegreen, violet, rose or olivaceous, microscopic, usually of 2–16 cells. Cells hemispherical with flattened adjacent faces after division, becoming globose-truncate or sometimes spherical, (8–) 12–50 microns in diameter. Cells irregularly arranged

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PLATE I

Vol. I, Minneapolis, U. of Minn. Press, pp. 1–328, 20 plates.

FIG. 1. *Anacystis aeruginosa,* small colony. X 675

2, 3. *Anacystis dimidiata,* two-celled and four-celled colonies. X 830

4, 5. *Entophysalis deusta,* a filament from within a shell and two filaments with emergent tips. X 550

6, 7. *Entophysalis conferta,* optical section and surface view of colony. X 1550

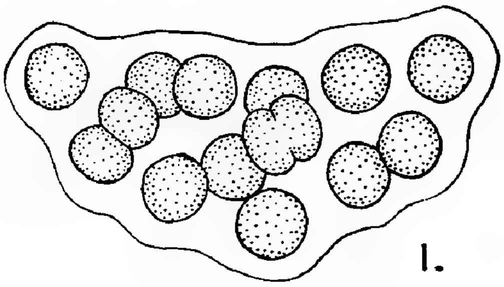
8. *Oscillatoria nigro-viridis,* end of filament. X 975

9. *Oscillatoria subuliformis,* end of filament. X 725

10. *Spirulina major,* filament. X 1400

11. *Spirulina subsalsa,* forma oceanica, filament. X 1400

(Figures 10 and 11 drawn by Joanna Woodson Parrish.)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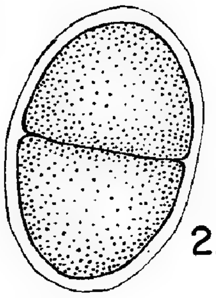
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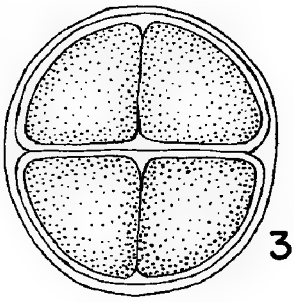
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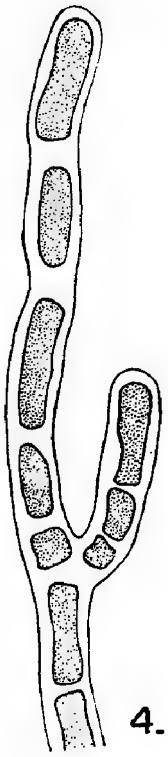
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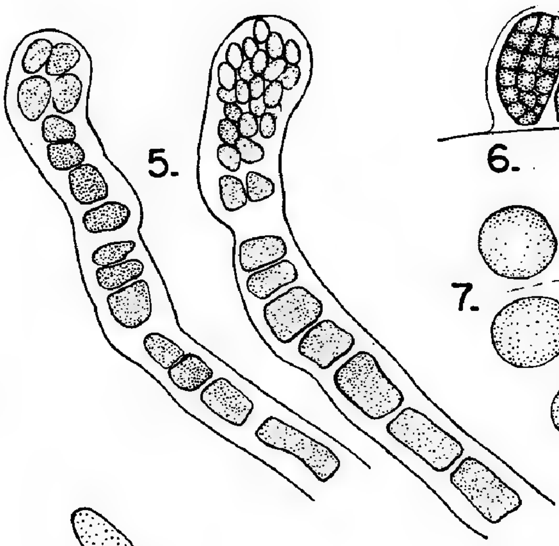
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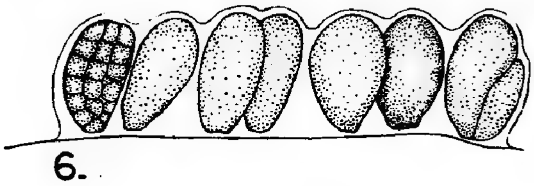
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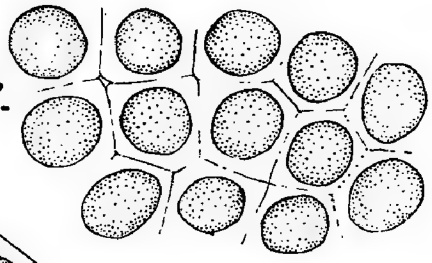
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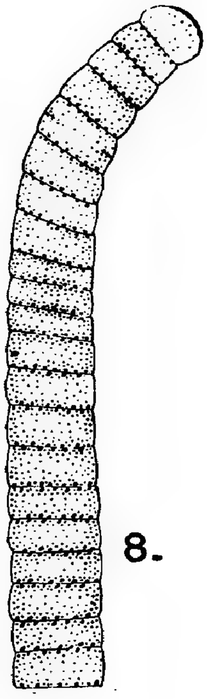
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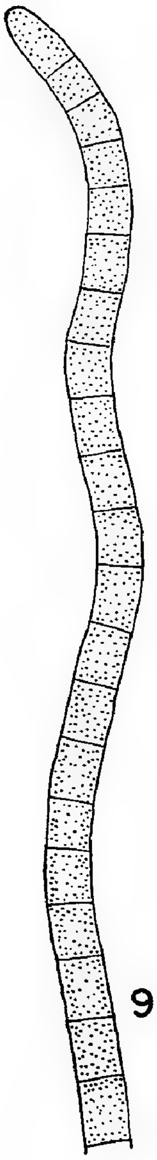
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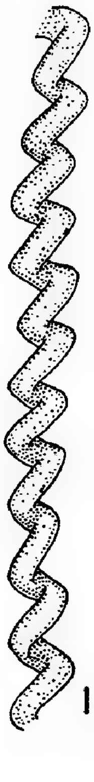
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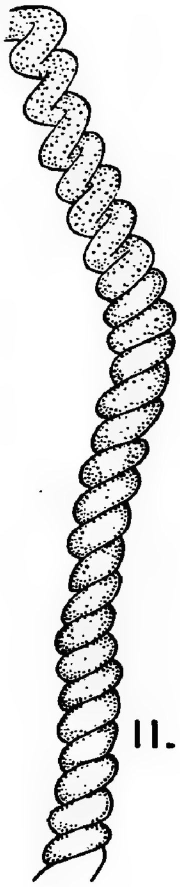
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within the sheath which is hyaline (rarely pale yellow), thin, homogeneous or somewhat lamellose. Protoplast bluegreen, violet, rose, or olivaceous, sometimes with a few coarse granules.

On or among other algae, rock breakwater and sunken iron barge near Fort Massachusetts.

Reference: Drouet and Daily, 1956, p. 70.

Anacystis marina (Hansgirg) Drouet and Daily

Plants bright bluegreen, at first microscopic and spherical or ovoid, later forming a gelatinous, macroscopic stratum. Cells subspherical and with flattened adjacent faces after division, becoming spherical, 0.5–2 microns in diameter, irregularly distributed and sometimes crowded within the sheath which is hyaline, homogeneous, diffluent. Protoplast bluegreen, homogeneous.

On older parts of *Hypnea musciformis*, rock breakwater near Ship Island lighthouse. Cells in a common gelatinous matrix.

Reference: Drouet and Daily, 1956, p. 44.

Family Chamaesiphonaceae

Entophysalis deusta (Meneghini) Drouet and Daily (Plate 1, Figs. 4 and 5).

Plant forming microscopic or macroscopic strata or cushions, on rocks, wood, and shells; bluegreen, olive, violet, rose, brown or black, firm or soft or becoming viscous by hydrolysis of the sheath. Solitary cells spherical, ovoid, or pyriform to 10 microns in diameter. Cells in a cushion or stratum, polyhedral after division, later spheroid, (1–) 3–6 microns in diameter. Cells within the substratum spherical, ovoid polyhedral, or cylindrical and in the form of a filament which is usually uniseriate, sometimes multiseriate (1–) 2–15 microns in diameter. Endosporangia spherical to ovoid, to 30 microns in diameter. Sheath at first hyaline, becoming brownish or (rarely) reddish or bluish, homogeneous or lamellose. Protoplast bluegreen, olive, yellow, violet, or red, usually homogeneous.

At all stations, especially common on and within old shells.

Reference: Drouet and Daily, 1956, p. 103.

Entophysalis conferta (Kützing) Drouet and Daily (Plate 1, Figs. 6 and 7).

Plants endophytic or epiphytic, microscopic or macroscopic, at first unicellular, later producing a cushion or stratum. Solitary cells spherical, ovoid, or pyriform, to 20 microns in diameter. Cells in a stratum or cushion spheroid after division, becoming spherical or polyhedral by crowding, (1–) 3–6 microns in diameter. Cells of endophytic filaments spherical, ovoid, cylindrical, or polyhedral, 3–8 microns in diameter. Endosporangia to 50 microns in diameter, solitary or aggregated. Protoplast bluegreen, olive, violet, or red, homogeneous or with fine granules.

On and within the outer layer of larger algae at all stations.

Reference: Drouet and Daily, 1956, p. 111.

ORDER OSCILLATORIALES

Family Oscillatoriaceae

Oscillatoria nigro-viridis (Thwaites) Gomont (Plate 1, Fig. 8).

Plant mass dark olive green. Trichomes 7–11 microns in diameter, the cells 3–5 microns long; constricted at the nodes; apex of trichome tapering, obtuse, the apical cell convex, without calyptra. Transverse walls frequently with granules.

On old shells in the intertidal zone, inner beach of Ship Island; Biloxi Bay near the Biloxi oyster laboratory.

References: Tilden, 1910, p. 69; Gomont, 1892, p. 237.

Oscillatoria subuliformis (Thwaites) Gomont (Plate 1, Fig. 9).

Plant mass dull green. Trichomes 4.7 to 6.5 microns in diameter, undulating, not constricted at the nodes. Apex of trichome tapering notably, apical cell obtuse, not capitate, without calyptra. Cells 4.7 to 6.5 microns long, apical cell longer. Protoplast finely granular with a few large refringent granules.

Intertidal zone and below, pier pilings near Fort Massachusetts, and on Ship Island Pass channel buoys; on rocks near Biloxi oyster laboratory.

References: Tilden, 1910, p. 77; Gomont, 1892, p. 246.

Spirulina major Kützing (Plate 1, Fig. 10).

Trichomes 1.2 to 1.7 microns in diameter forming a loose but regular spiral 2.5 to 5 microns wide with 2.7 to 5 microns space between the turns. Usually scattered among other algae.

Occasional as isolated filaments from scrapings off the sunken iron barge near Fort Massachusetts and from the buoys in Ship Island Pass.

References: Tilden, 1910, p. 87; Gomont, 1892, p. 271.

Spirulina subsalsa Oersted, forma *oceanica* (Crouan) Gomont (Plate 1, Fig. 11)

Plant mass bright bluegreen. Trichomes 1–2 microns in diameter forming a tight spiral 3–5 microns wide of contiguous turns or nearly so.

Forming small but conspicuous patches a few mm. in diameter on rocks and a sunken iron barge near Fort Massachusetts, and on buoys in Ship Island Pass.

References: Tilden, 1910, p. 89; Gomont, 1892, p. 273.

Lyngbya confervoides C. Agardh (Plate II, Fig. 1).

Plant mass blackish green or yellowish green, forming a leathery sheet on rocks and pilings. Trichomes 9–25 microns in diameter, the cells 2–4 microns long, the transverse walls usually granulated. Trichomes not constricted at the nodes, not tapering or capitate, the apical cell rotund. Sheaths thick, colorless, becoming lamellose, roughened, and yellowish. Protoplast olive or bluegreen.

Common at nearly all stations, especially on intertidal rocks and pilings. Often abundant on creosoted pilings where it may be the only bluegreen.

References: Tilden, 1910, p. 119; Gomont, 1892, p. 156.

Lyngbya epiphytica Hieronymus (Plate II, Fig. 3).

Filaments less than 2 microns wide, the sheath thin, inconspicuous. Typically wound spirally around filamentous algae.

Spirally wound around the filaments of *Ectocarpus mitchellae* from rocks of the breakwater near Fort Massachusetts.

Dr. Francis Drouet has expressed doubt (*in litt.*) that this is a valid species, and suggests that it may be a species of *Phormidium* with a predilection for spiraling around filaments or branches of larger algae. Solution of the question must await reexamination of the type material.

Reference: Howe, 1920, p. 622.

Lyngbya lutea (C. Agardh) Gomont (Plate II, Fig. 2).

Plant mass yellowish brown or olive, the filaments coiled or entangled. Trichomes 2.5 to 6 microns in diameter, the cells 1.5 to 5.5 microns long. Apex of trichomes not tapering, apical cell with a rotund calyptra; transverse walls indistinct, nodes not constricted. Protoplast olive green, granular.

St. Louis Bay near Cedar Point; Back Bay near Keesler Field; municipal pier, Ocean Springs; Biloxi oyster laboratory.

References: Tilden, 1910, p. 114; Gomont, 1892, p. 161.

Lyngbya semiplena (C. Agardh) J. Agardh (Plate II, Fig. 4).

Plants forming a skin on stones and pilings in the intertidal zone and below. Trichomes 5–12 microns in diameter, not constricted at the joints, apex slightly tapering, capitate, apical cell with a calyptra. Cells 2–3 microns long, transverse walls granulated. Sheaths thick, colorless, becoming lamellose.

On pilings and rocks at all stations in the intertidal zone. Evidently the most abundant bluegreen.

References: Tilden, 1910, p. 118; Gomont, 1892, p. 158.

Lyngbya aestuarii (Mertens) Liebmann (Plate II, Fig. 5).

Plant mass blackish or dull bluegreen, varying in nature with the habitat. Trichomes 8–24 microns in diameter, the cells 2.7 to 5.6 microns long, contents bluegreen or olive, granular. Trichomes not constricted at the nodes, the apex slightly tapering and capitate, the apical cell with a thin calyptra.

St. Louis Bay near Cedar Point.

References: Tilden, 1910, p. 120; Gomont, 1892, p. 147.

Phormidium submembranaceum (Ardissone & Strafforello) Gomont (Plate II, Fig. 7).

Plant mass membranaceous, leathery, dark green, typically as circular patches on stones or woodwork, intertidal and below. Trichomes 5 microns in diameter, constricted at the joints, with apex straight, tapering, capitate, apical cell with calyptra. Cells 4–10 microns long, the contents homogeneous, bluegreen. Filaments densely entangled within an amorphous gelatinous matrix.

Forming patches in the splash zone on buoys in Ship Island Pass; Biloxi Bay near the Biloxi oyster laboratory.

References: Tilden, 1910, p. 104; Gomont, 1892, p. 200.

Trichodesmium thiebautii Gomont (Plate II, Fig. 8).

Colonies amber, at least giving an amber color to water where heavy accumulations occur at the surface, green in dried material. Habitat exclusively as marine plankton in the form of fasciculate bundles of filaments, the fascicles 2–6 mm in length, filaments in

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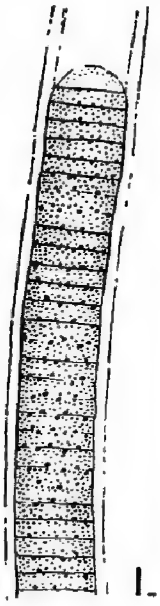
PLATE II

FIG. 1. *Lyngbya confervoides,* end of filament. X 450

2. *Lyngbya lutea,* end of filament. X 1430
3. *Lyngbya epiphytica,* filament enwrapping a branch of *Ectocarpus.* X 1100
4. *Lyngbya semiplena,* end of filament. X 600
5. *Lyngbya aestuarii,* end of filament. X 340
6. *Nodularia harveyana,* two filaments. X 1100
7. *Phormidium submembranaceum,* end of filament. X 990 (After Gomont, 1892).
8. *Trichodesmium thiebautii,* end of filament. X 275
9. *Microcoleus tenerrimus,* end of trichome. X 1375 (After Gomont, 1892.)
10. *Microcoleus chonoplastes,* end of trichome. X 775 (After Gomont, 1892.)
11. *Symploca atlantica,* showing false branching. X 775 (After Gomont, 1892.)

(Figures 6, 9, 10, and 11 drawn by Joanna Woodson Parrish.)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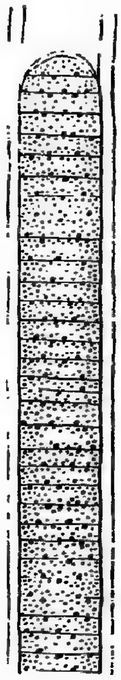
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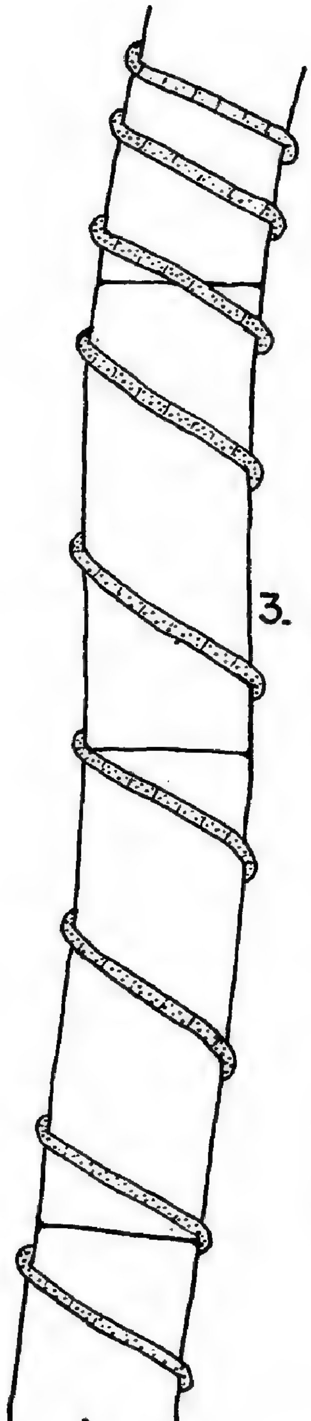
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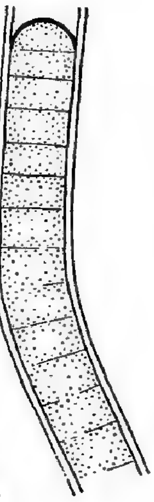
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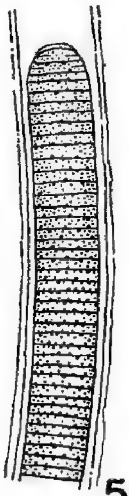
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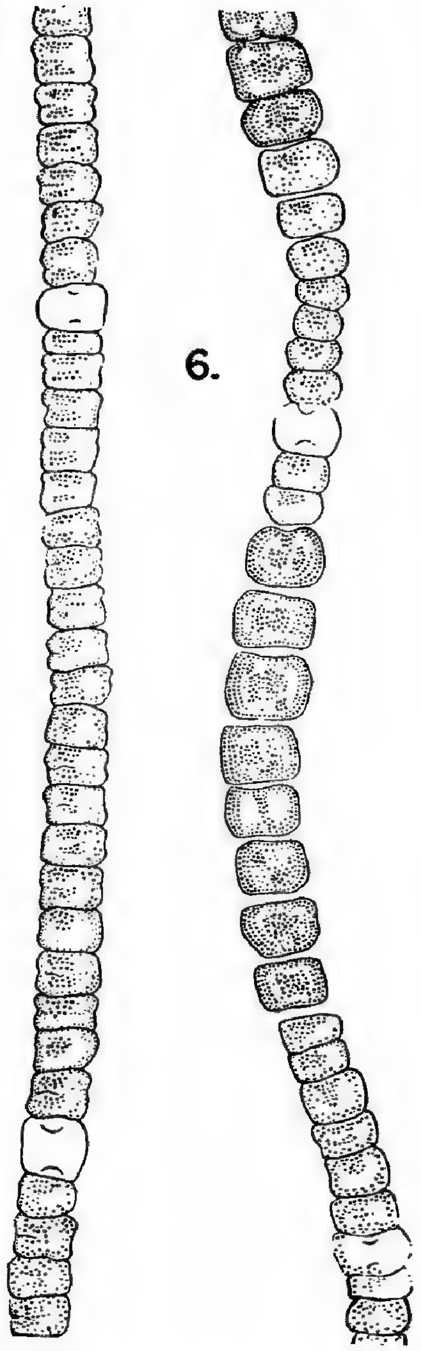
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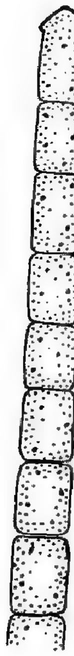
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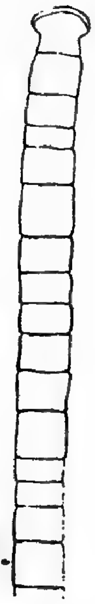
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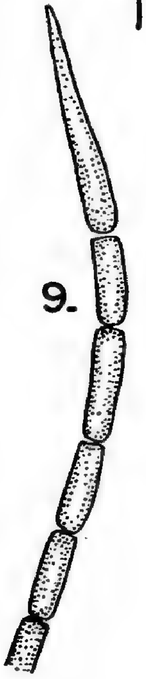
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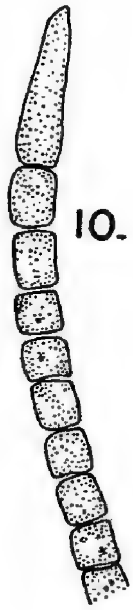
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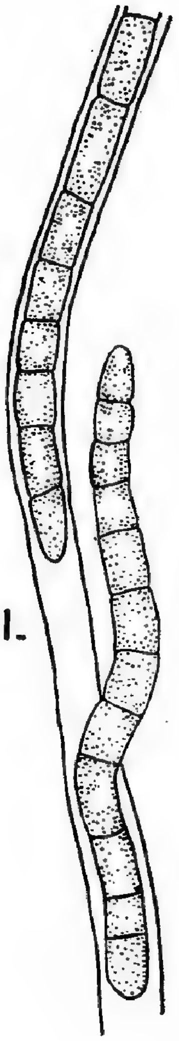
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the center of the colony twisted, rope-like, free at the ends. Trichomes 7–16 microns in diameter, not constricted at the nodes, with apex briefly tapering; cells 8–26 microns long, protoplast granular with larger granules at the endwalls.

Forming extensive amber patches on the water, Gulf side of Ship Island, July 19, 1954. Probably of occasional occurrence in Mississippi Sound each summer.

Dr. Francis Drouet prefers the name *Oscillatoria thiebautii* (Gomont) Geitler for this species, although, as he points out, *Trichodesmium* Ehrenberg has been conserved in the International Code of Botanical Nomenclature (1956).

References: Tilden, 1910, p. 84; Gomont, 1892, p. 217.

Symploca atlantica Gomont (Plate II, Fig. 11).

Plant mass blackish or brownish green forming a fine turf with fascicles of filaments to 1 cm. high. Filaments single within a thin sheath, unbranched. Trichomes 4–6 microns in diameter, cells 2–6 microns long with distinct but not granulated crosswalls and yellow-green protoplast, apical cell with calyptra. Trichomes with constricted nodes.

Abundant on the upper surface of a sunken iron barge, somewhat exposed or awash at low tide, north side of Fort Massachusetts; between Bay St. Louis and Waveland, mainland side.

References: Tilden, 1910, p. 129; Gomont, 1892, p. 129.

Hydrocoleum lyngbyaceum Kützing (Plate III, Figs. 1 and 2).

Plant mass as bluegreen patches; trichomes several within the sheath, producing false branches in upper portions; sheaths wide, soft, roughened in outline, tapering or open at the end, sometimes diffluent. Trichomes 8–16 microns in diameter, cells 2.5 to 4.5 microns long, not constricted at the nodes, apex of trichome tapering, truncate; transverse walls granulated. Trichomes often single in the sheath in upper parts.

Producing characteristic, bright bluegreen patches on the sides of a sunken iron barge near Fort Massachusetts, and on barnacles from buoys in Ship Island Pass.

References: Tilden, 1910, p. 135; Gomont, 1892, p. 75.

Microcoleus chthonoplastes (Flora Danica) Thuret (Plate II, Fig. 10).

Filaments many within a sheath, twisted, forming a dull, green, compact, stratified mass. Trichomes 2.5 to 6 microns in diameter, the cells 3.6 to 10 microns long, constricted at the nodes, the apex tapering, apical cell acute-conical.

Among *Spartina alterniflora*, salt marsh, Ship Island; Biloxi Bay near Biloxi oyster laboratory; near municipal pier, Ocean Springs.

References: Tilden, 1910, p. 155; Gomont, 1892, p. 91.

Microcoleus tenerrimus Gomont (Plate II, Fig. 9).

Filaments many within a sheath, rather loosely aggregated; plant mass gray or dull green or mixed with other algae. Trichomes 1.5 to 2 microns in diameter, cells 2.2 to 6 microns long, constricted at the nodes; apex of trichome gradually tapering, apical cell acute-conical.

PLATE III

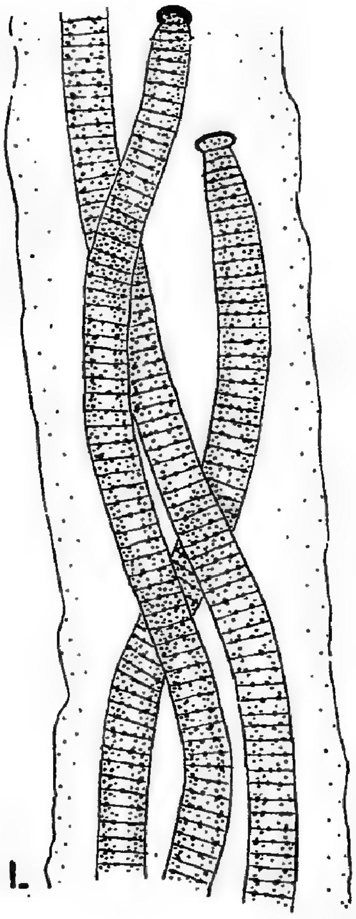
FIGS. 1, 2. *Hydrocoleum lyngbyaceum*, several filaments within a sheath and a single filament within a sheath. X 360

3. *Mastigocoleus testarum*, portion of plant from decalcified shell showing a flagelliform branch and a branch with terminal heterocyst. X 550

4. *Plectonema terebrans*, filament with false branches. X 2200 (After Bornet and Flahault)

5. *Amphithrix violacea*, portion of basal layer with erect filaments. X 1650

6. *Plectonema nostocorum*, filament with branch. X 2500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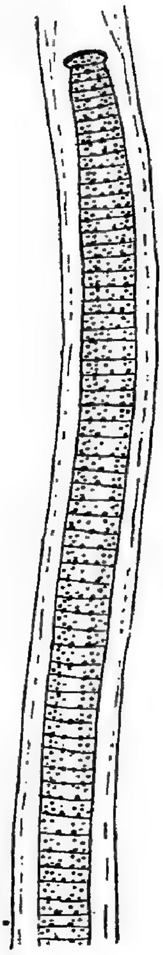
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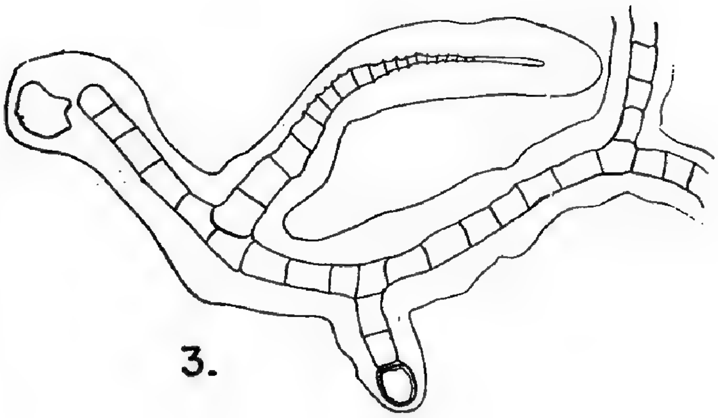
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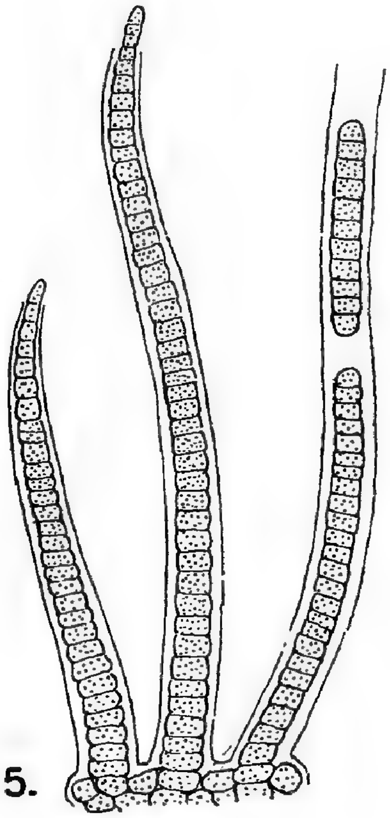
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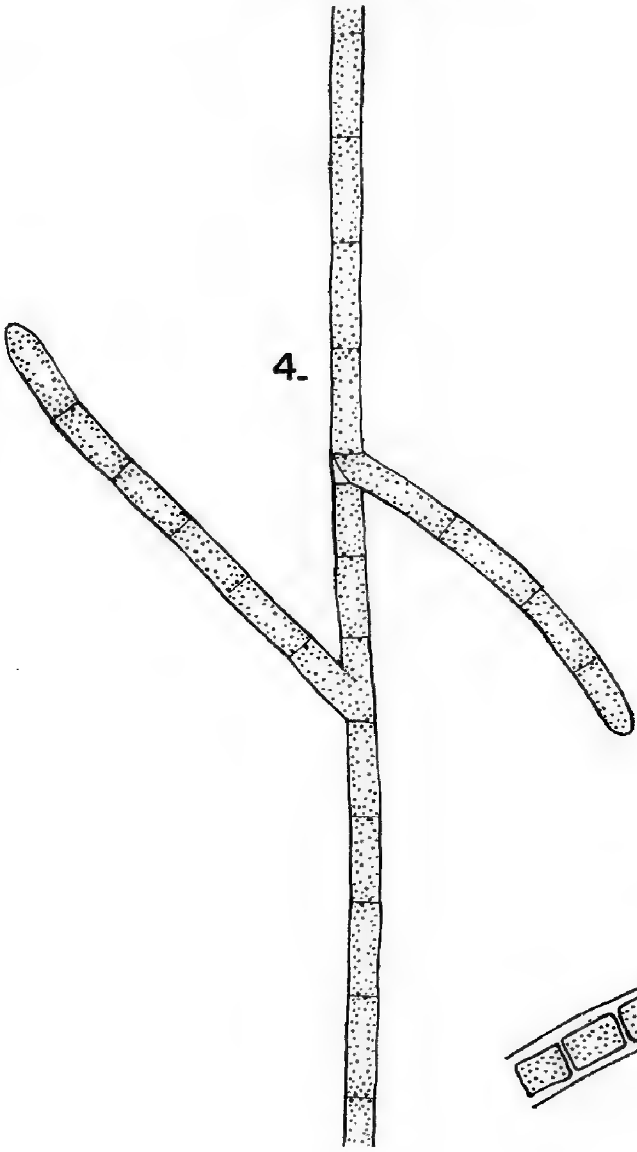
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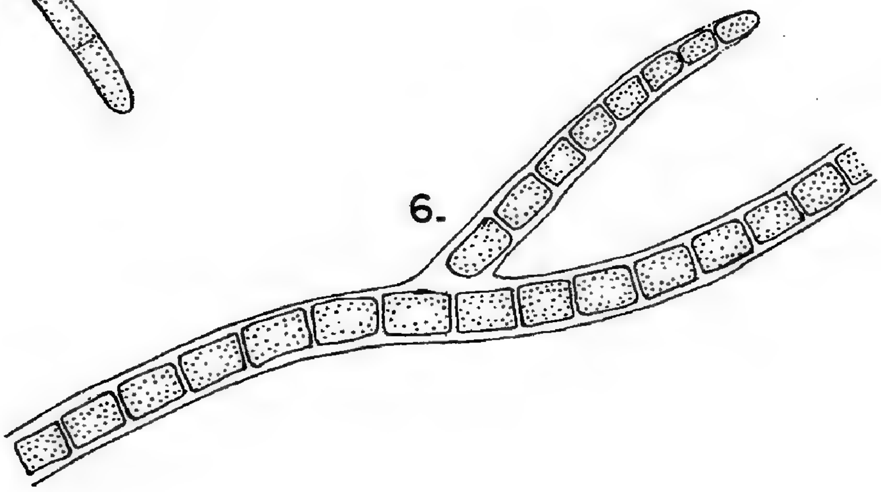
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Mississippi Sound between Bay St. Louis and Waveland; St. Louis Bay near Cedar Point; near the municipal pier, Ocean Springs; municipal pier, Gulfport; Back Bay near Keesler Field; Biloxi Oyster Laboratory.

References: Tilden, 1910, p. 155; Gomont, 1892, p. 93.

Plectonema nostocorum Bornet (Plate III, Fig. 6).

Filaments with numerous false branches, the trichomes single in very thin sheaths; plant mass thin and flat, dull green. Trichomes slender, 1 to 1.5 microns in diameter, constricted at the nodes, cells 2 to 2.5 microns long, apical cell rotund. Cells not granular.

Near the Biloxi oyster laboratory, Biloxi Bay.

References: Tilden, 1910, p. 209; Gomont, 1892, p. 122.

Plectonema terebrans Bornet and Flahault (Plate III, Fig. 4).

Similar to *P. nostocorum* except that it usually bores into shells or limestone (although it may develop at the surface). Cells 2–6 microns long, not constricted at the nodes, with two refringent granules at the crosswalls.

Penetrating oyster shells from pier pilings near Fort Massachusetts, Ship Island.

References: Tilden, 1910, p. 209; Gomont, 1892, p. 123.

Family Nostocaceae

Nodularia harveyana (Thwaites) Thuret (Plate II, Fig. 1).

Filaments 6–7 microns in diameter, unbranched, with a thin sheath, intercalary heterocysts and gonidia; cells before division about as long as broad; filaments tapering slightly at the apex (but not long tapering or hair tipped as in *Calothrix*). Gonidia 8 microns in diameter, in a series, remote from the heterocysts.

In a salt marsh near Cedar Point, Bay St. Louis.

References: Tilden, 1910, p. 182; Bornet and Flahault, 1888, p. 243.

Family Stigonemaceae

Mastigocoleus testarum Lagerheim (Plate III, Fig. 3).

Plants on the surface and penetrating old shells, the filaments producing branches of two kinds, one cylindrical, the other tapering flagelliform; heterocysts present, usually single; trichomes single within the sheath, except in the branches, protoplast homogeneous.

Mississippi Sound between Bay St. Louis and Waveland, boring in old shells.

References: Tilden, 1910, p. 237; Bornet and Flahault, 1887, p. 54.

Family Rivulariaceae

Amphithrix violecea (Kützing) Bornet and Flahault (Plate III, Fig. 5).

Plant mass of fasciculate filaments arising from a basal layer of interwoven filaments, brownish red or violet, the filaments 2–3 microns in diameter, 1–3 mm. tall, sheaths

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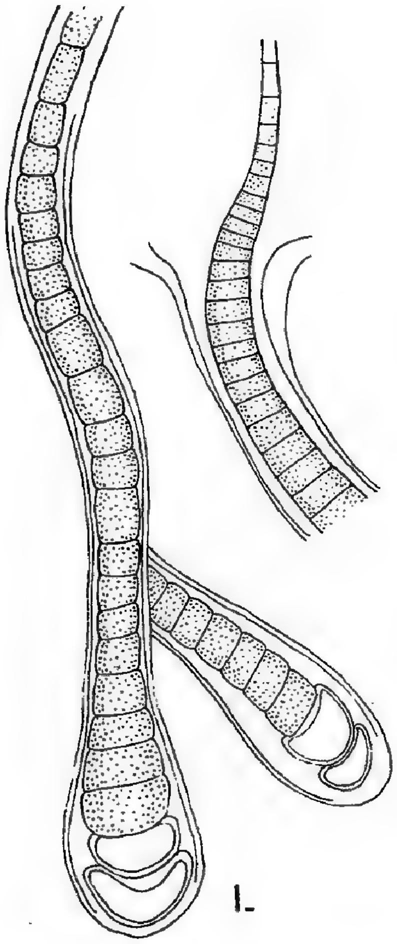
PLATE IV

FIG. 1. *Calothrix confervicola.* X 550 (After Taylor, 1928)
2. *Calothrix crustacea.* X 375 (After Taylor, 1928)
3. *Stichococcus marinus.* X 800
4, 5. *Ulvella* lens, a young plant and the margin of a large plant. X 1100
6. *Entocladia viridis,* portion of plant from surface of Padina. X 550
7. *Ulva lactuca,* cross section of plant. X 300

(Figures 1 and 2 drawn by Joanna Woodson Parrish.)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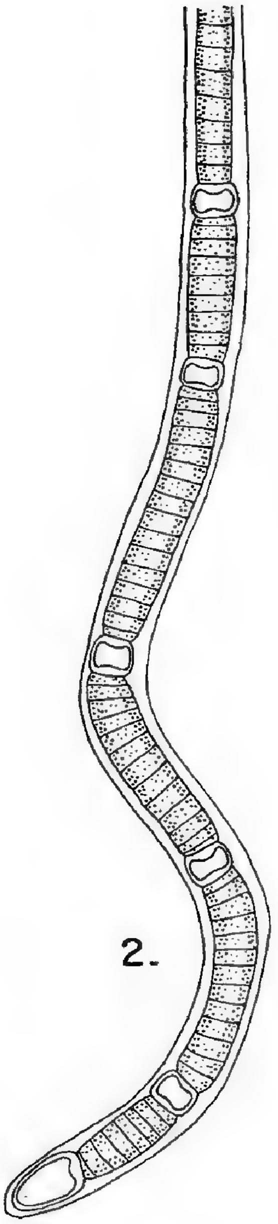
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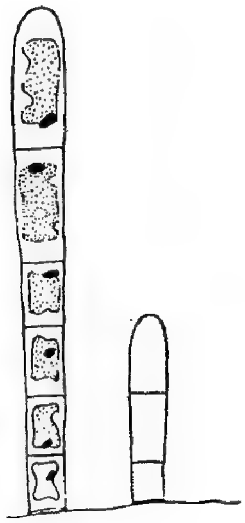
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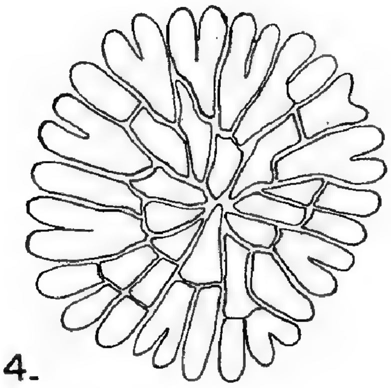
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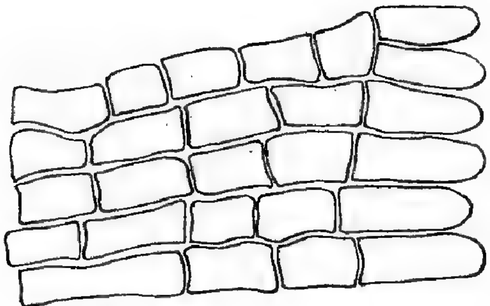
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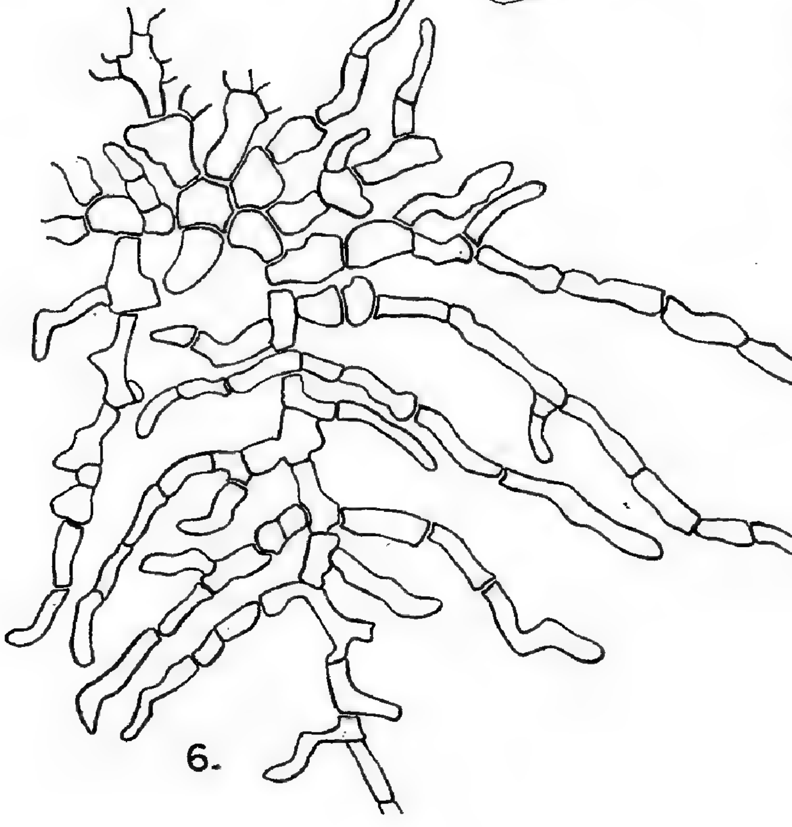
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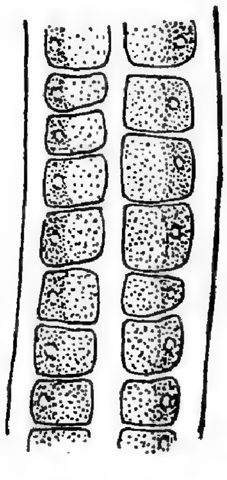
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thin. Trichomes constricted at the nodes with cells shorter than wide, the protoplast granular. Heterocysts not produced. Branches confined to the basal filaments.

Biloxi Bay near the Biloxi oyster laboratory.

References: Tilden, 1910, p. 253; Bornet and Flahault, 1886, p. 344.

Calothrix crustacea Thuret (Plate IV, Fig. 2).

Plant mass of penicillate tufts 1–2 mm. tall, the filaments with basal and intercalary heterocysts, usually unbranched, sheaths colorless or yellowish, thick, becoming lamellose. Trichomes 8–15 microns in diameter, tapering to a long hair; cells short; hormogones numerous, 4 or 5 times longer than wide; gonidia oblong, cylindrical, in a series.

Mississippi Sound near the Biloxi lighthouse.

References: Tilden, 1910, p. 264; Bornet and Flahault, 1886, p. 359.

Calothrix confervicola[1] (Roth) C. Agardh (Plate IV, Fig. 1).

Plant mass of penicillate tufts to 1 mm. tall, the filaments with basal heterocysts only, sheaths colorless or yellowish becoming lamellose. Trichomes 8–15 microns in diameter tapering to a hair. Hormogones numerous, 4 to 5 times longer than wide.

Mississippi Sound between Bay St. Louis and Waveland; St. Louis Bay near Cedar Point; near the Biloxi lighthouse; near the municipal pier, Ocean Springs.

References: Tilden, 1910, p. 258; Bornet and Flahault, 1886, p. 353; Fan, 1956.

CHLOROPHYTA

ORDER ULOTRICHALES

Family Ulotrichaceae

Stichooccus marinus (Wille) Hazen (Plate IV, Fig. 3).

Filaments erect, unbranched, 5–6 microns in diameter, the cells 1–2 diameters long, chromatophore a round or oblong plate extending less than halfway around the cell, pyrenoid indistinct(?).

Near Biloxi oyster laboratory, Biloxi Bay.

Reference: Taylor, 1937, p. 45.

Family Chaetophoraceae

Entocladia viridis Reinke (Plate IV, Fig. 6).

Plants endophytic, filamentous, creeping within the gelatinous coating of host plants, branching arborescent, the cells variable in length and width, mostly 3–6 microns wide, 1–6 diameters long, hairs not produced.

Abundant on many algae, especially *Padina vickersiae,* rock breakwater near Fort Massachusetts.

References: Taylor, 1937, p. 53; Collins, 1909, p. 279.

Phaeophila floridearum Hauck (Plate V, Fig. 1).

Plants creeping, epiphytic or endophytic in the gelatinous membrane of the host, filamentous, irregularly branched, the cells 9–40 microns wide, 15–50 microns long, cylindrical to irregular, some cells producing erect colorless, zig-zag or slightly spiral hairs without crosswalls.

Common on *Hypnea musciformis* and other algae, breakwater near Fort Massachusetts.

References: Taylor, 1928, p. 58; 1937, p. 51.

Ulvella lens Crouan (Plate IV, Figs. 4 and 5).

Plants forming a disk 0.1 to 1.0 mm. in diameter, of closely-appressed, radiating filaments except at the center. Cells of the radial filaments mostly 2–5 microns in diameter (to 6) and elongate-rectangular in shape (occasionally square), 5–12 microns long (to 20). Disk monostromatic in the radiating portion, but several cells thick at the center where the cells are irregular in arrangement, as seen from above, and more or less rounded. Central cells of larger disks to about 10 microns in diameter. Chromatophore a parietal disk filling the entire cell.

Common on the basal leaves of *Sargassum filipendula* rock breakwater near Fort Massachusetts.

The description of *Ulvella lens* in De Toni, *Sylloge Algarum,* Vol. I, p. 148, is actually a combination of the original description and a determination by Hansgirg (1887), which was not in full agreement with the original description. Huber (1892) has discussed this problem and expresses the opinion that Hansgirg may have been dealing with the young basal disk of some larger alga, a possibility that Hansgirg himself considered. It is the writers' opinion that Hansgirg actually had a species of *Ulvella* other than *lens.*

Material of *Ulvella lens* reported by Børgesen (1913) and Newton (1931) is in excellent agreement with Crouan's original description. However, that reported by Hoyt (1917–18) and Taylor (1928) had radial cells 10–15 microns in diameter and probably should be regarded as another species.

Crouan reported *Ulvella lens* on stones and shells and also as an epiphyte; hence the inference by Collins (1909) that it is restricted to stones and shells is probably incorrect. More recent authors have reported it from both types of habitats.

ORDER ULVALES

Family Ulvaceae

Enteromorpha flexuosa J. Agardh (Plate V, Fig. 4).

Plant tubular, unbranched, tapering to the base, cells in longitudinal rows, thick-walled; plants in tufts, upper end of the tube to 5 mm. wide.

Occasional tufts on rocks, pilings near Fort Massachusetts.

References: Collins, 1909, p. 203; Taylor, 1928, p. 55; 1954, p. 93.

Enteromorpha lingulata J. Agardh

Plants in tufts or turf-forming to 7 cm. tall, usually branched from near the base, cells in longitudinal rows.

Abundant in short tufts at the waterline and in scattered tufts below the waterline on the buoys in Ship Island Pass. Occasional on rocks and the submerged iron barge near Fort Massachusetts. This was the most common *Enteromorpha* and agreed well with the summer phase of this species at Beaufort, N.C. (Pew, 1941). The genus, however, is poorly represented in the summer here. Several other species are undoubtedly present during winter months.

Reference: Newton, 1931, p. 69.

Enteromorpha plumosa Kützing

Plant tubular, much-branched, the branches terminating in a single series of cells, the chromatophore not filling the cell.

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[1] A revision of the genus *Calothrix* (Fan, 1956) appeared while this paper was in press. Material included here would have been associated with *C. scopulorum* (Weber & Mohr) C. Agardh prior to Fan's revision. Typical material of *scopulorum* is apparently regarded by Fan as belonging to the species *confervicola,* although he has not yet published the synonmy.

Occasional as very small plants easily overlooked on the rocks near Fort Massachusetts, Ship Island.

References: Collins, 1900, p. 198; Taylor, 1928, p. 56; 1954, p. 93.

Ulva lactuca Linnaeus (Plate IV, Fig. 7).

Plant an expanded membrane two cells thick, the blade about 60 microns thick throughout.

Common on rocks near Fort Massachusetts, evidently only var. *rigida* (C. Agardh) LeJolis, which grew usually in crisp tufts. Occasional also on the Ship Island Pass buoys. The variety is characterized by cells that are taller than wide.

References: Collins, 1909, p. 214; Hoyt, 1917–18, p. 421; Taylor, 1954, p. 94.

ORDER CLADOPHORALES

Family Cladophoraceae

Cladophora fascicularis (Mertens) Kützing (Plate V, Fig. 5).

Plants filamentous, much-branched, to 1 foot tall or more (in some habitats), the main axes to 360 microns in diameter, the ultimate branches in fasciculate groups.

On rocks and a sunken iron barge near Fort Massachusetts and on the buoys of Ship Island Pass. Typically a species of wave-beaten localities but not confined to such habitats.

References: Collins, 1909, p. 345; Taylor, 1928, p. 62.

Cladophora gracilis (Griffiths) Kützing (Plate V, Figs. 2 and 3).

Plants filamentous, much-branched, the main axes rarely over 150 microns wide, the branches successively more slender, the ultimate branches in secund series, 40–60 microns in diameter. Cells 3–5 diameters long throughout.

Around the base of *Spartina alterniflora* in a salt marsh, Ship Island. Occasional on rocks around Fort Massachusetts. Typically a species of salt marshes, intertidal if shaded, and in water of lower salinity than most other species of *Cladophora*. This species is extremely variable.

References: Collins, 1909, p. 342; Taylor, 1937, p. 89.

Rhizoclonium riparium (Roth) Harvey (Plate VI, Fig. 1).

Filamentous, usually unbranched though occasionally with short, rhizoid-like branches; cells 15–30 microns in diameter, 1–2 diameters long. A plant of salt marshes or muddy substrata and usually in brackish water.

In a salt marsh, Ship Island; on sticks and woodwork, intertidal zone at Marsh Point near Ocean Springs; widely distributed in Mississippi Sound.

References: Collins, 1909, p. 327; Taylor, 1954, p. 95.

PLATE V

FIG. 1. *Phaeophila floridearum*, portion of a plant. X 275

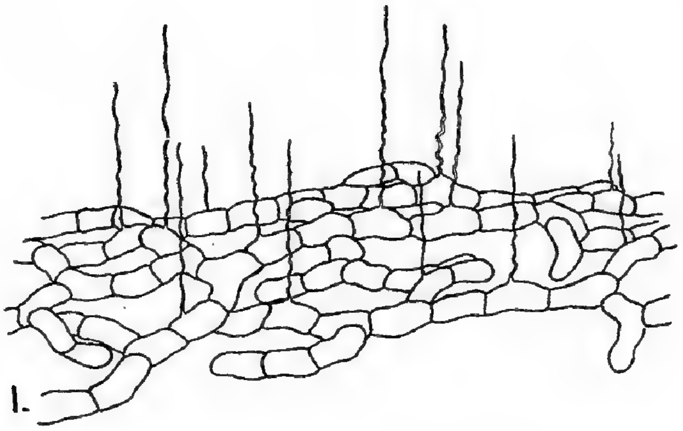
2, 3. *Cladophora gracilis*, branching habit of plant and enlarged portion showing a few secund ultimate branches. X 2 and X 12

4. *Enteromorpha flexuosa*, habit of a cluster of plants. X 2

5. *Cladophora fascicularis*, habit of plant. X 1.5

6. *Ostreobium quekettii*, portion of plant from decalcified barnacle shell. X 400

(Figures 1 through 5 drawn by Sylvia A. Earle.)



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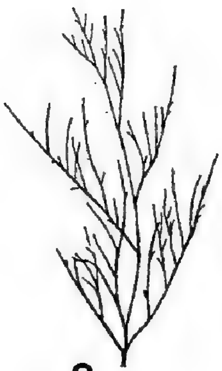

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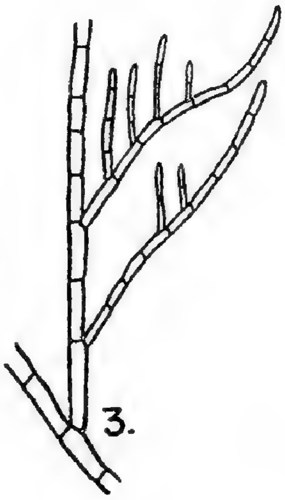

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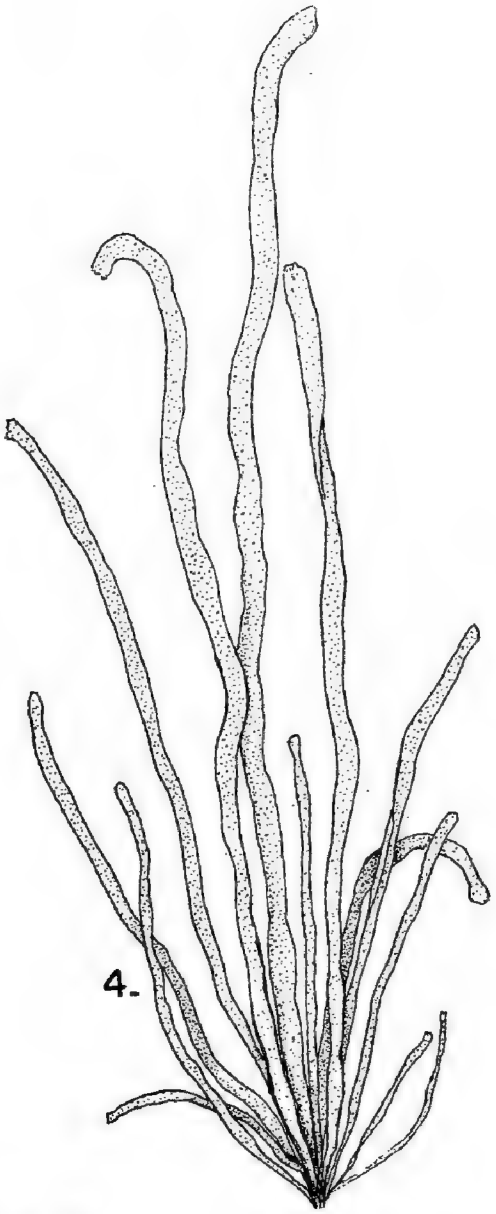

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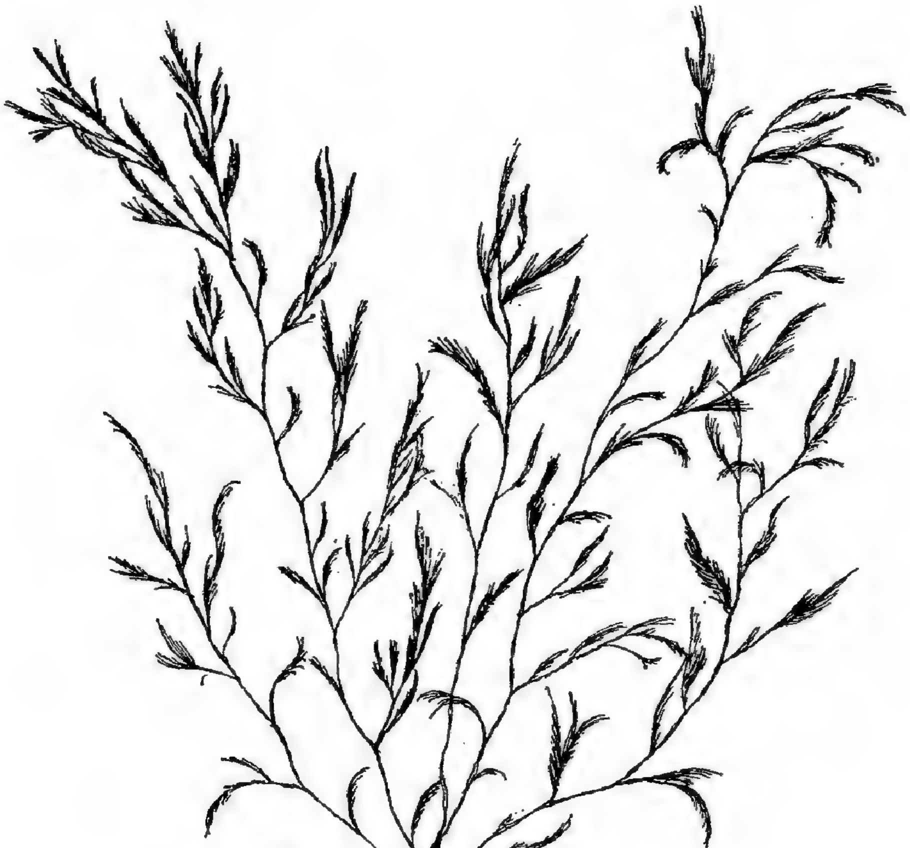

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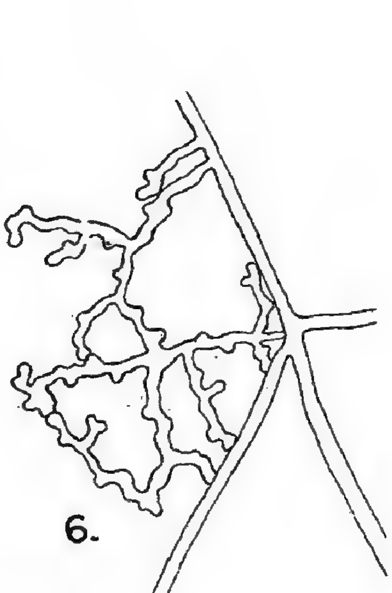

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ORDER SIPHONALES

Family Phyllosiphonaceae

Ostreobium quekettii Bornet and Flahault (Plate V, Fig. 6).

Plant penetrating old shells or limestone, of slender filaments 4–5 microns in diameter with many local inflations to 40 microns diameter or more.

From a dead barnacle shell on the side of a sunken iron barge near Fort Massachusetts.

References: Collins, 1900, p. 408; Taylor, 1937, p. 99.

CHRYSOPHYTA

ORDER HETEROSIPHONALES

Family Vaucheriaceae

Vaucheria thuretii Woronin

Plant filamentous, branched, coenocytic, typically partially embedded in mud; the filaments 30–120 microns wide, antheridia sessile, straight, oogonia spherical, stalked.

From near the Biloxi Oyster Laboratory, Biloxi Bay. Collected and determined by Dr. Francis Drouet.

Reference: Collins, 1909, p. 424.

PHAEOPHYTA

ORDER SPHACELARIALES

Family Sphacelariaceae

Sphacelaria tribuloides Meneghini (Plate VI, Figs. 2, 3, and 4)

Plants filamentous, polysiphonous except at the tips, forming erect, stiff tufts to about 5 mm. tall, the filaments 40–60 microns in diameter with a prominent apical cell. Reproduction by propagulae which are shield-shaped to triangular with two free arms.

On old basal leaves of *Sargassum filipendula* from the rock breakwater and on the sides of a sunken iron barge near Fort Massachusetts.

Reference: Taylor, 1928, p. 106.

Family Ectocarpaceae

Ectocarpus confervoides (Roth) LeJolis (Plate VI, Figs. 5, 6, and 7).

Plants filamentous, branched, 2–50 cm. tall, the gametangia short subulate or tapering somewhat at both ends, 10–40 microns in diameter, 60–400 microns long, usually sessile. A species of many forms.

PLATE VI

FIG. 1. *Rhizoclonium riparium,* portion of a filament. X 400

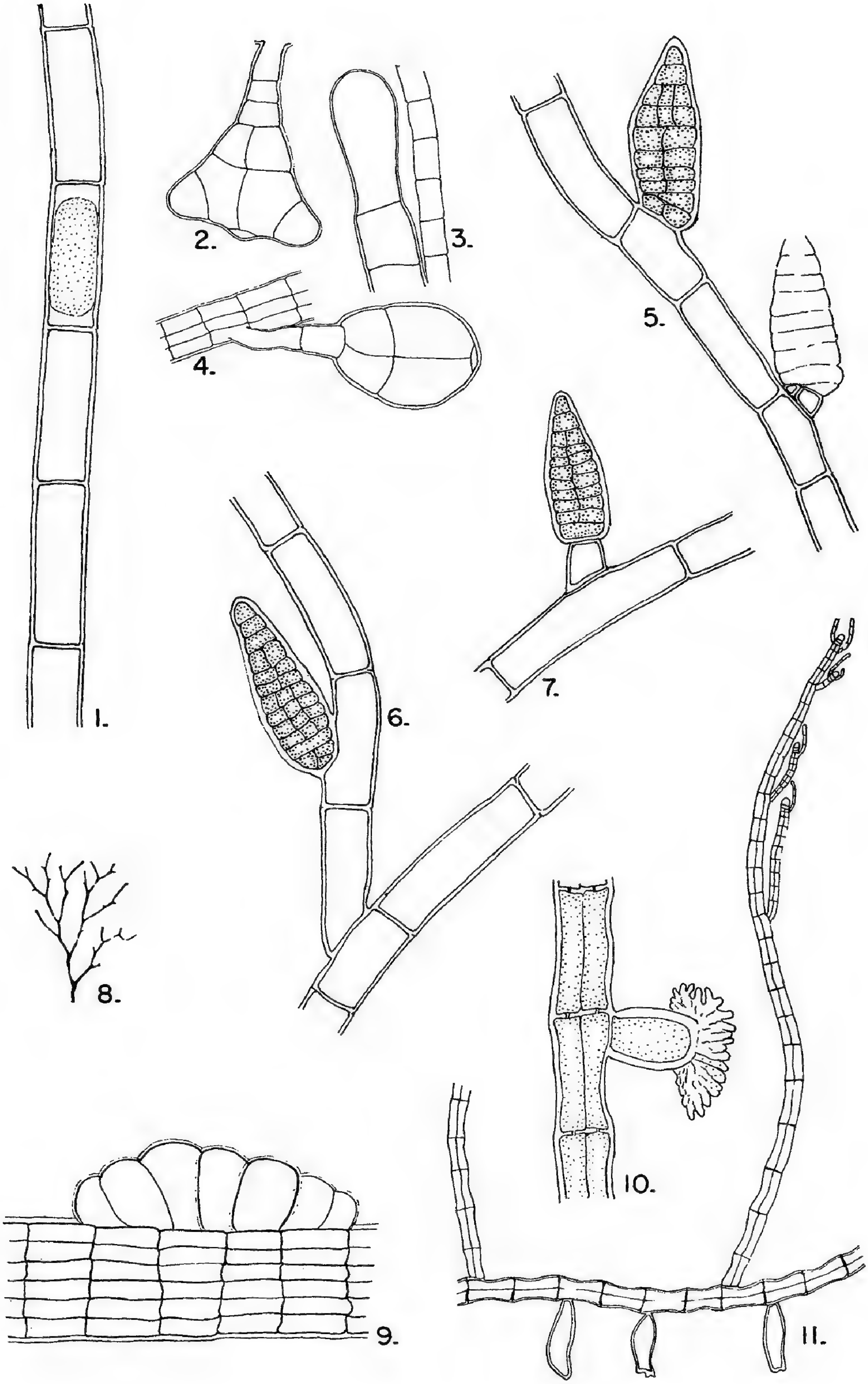
2, 3, 4. *Sphacelaria tribuloides,* a nearly mature propagulum, apical cell with hair, and young propagulum. X 130

5, 6, 7. *Ectocarpus confervoides* (forma ?), filaments with gametangia. X 700

8. *Dictyota cervicornis* (?), habit of plant. X ½

9. *Padina vickersiae,* cross section of plant through a group of oogonia. X 150

10, 11. *Lophosiphonia sacchoriza,* creeping filament with a coralloid rhizoid and habit of a portion of a plant with saccate rhizoids. X 150 and X 75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Common on the sunken iron barge and on larger algae from the rocks near Fort Massachusetts; on the buoys in Ship Island Pass. The gametangia of this material were similar to forma *typica* Kjellman. It is probably a summer form of a plant that looks quite different during winter months.

References: Rosenvinge and Lund, 1941, p. 21; Hoyt, 1917–18, p. 439.

Ectocarpus dasycarpus Kuckuck

Plants filamentous, branched, 5–7 cm. tall, branching somewhat dichotomous, main filaments 20–40 microns in diameter, the cells 2–3 times as long as wide. Gametangia usually terminal on short lateral branches, 10–20 microns in diameter, 60–150 microns (sometimes to 250) long, not hair-tipped.

Collected by Dr. Francis Drouet at Biloxi, December 1948 (Taylor, 1954), and possibly restricted to winter months. This species is regarded as a form of *E. confervoides* by Lund in Rosenvinge and Lund, 1941.

Ectocarpus duchassaignianus Grunow

Plants filamentous, branched, 2–3 cm. tall, the main filaments 20–22 microns in diameter. Gametangia 25–27 (to 50?) microns in diameter, 100–250 (mostly about 125) microns long, rounded or truncate at the apex, sessile.

On *Gelidium corneum*, north wall of Fort Massachusetts.

Reference: Hoyt, 1917–18, p. 437.

Ectocarpus elachistaeformis Heydrich ?

Filamentous, microscopic, lower filaments creeping producing erect, rarely branched filaments 1–2 mm. tall, 12–15 microns in diameter at the base. Gametangia borne at the base of the erect filaments, elongate, ascending.

Several small plants with the vegetative characteristics of this species were found on buoy 29, Ship Island Pass. In the absence of gametangia, the determination is uncertain.

Reference: Taylor, 1928, p. 107.

Ectocarpus mitchellae Harvey

Filamentous, 2–15 cm. tall, much-branched, the main filaments 35–45 (to 50) microns in diameter, the gametangia 15–20 microns in diameter and 70–100 microns long, elliptical-oblong with rounded apices, usually sessile.

Occasional on larger algae, rocks near the fort, and on sea grasses along the sound side of Ship Island.

Reference: Hoyt, 1917–18, p. 439.

Ectocarpus siliculosus (Dillwyn) Lyngbye

This species, characterized by hair-tipped gametangia and producing large plants has been reported for Mississippi Sound for the winter months (Taylor, 1954). How long it persists in the spring is not yet known. Rosenvinge and Lund, 1941, regard it as *E. confervoides*, forma *siliculosa* (Dillwyn) Kjellman.

ORDER DICTYOTALES

Family Dictyotaceae

Dictyota dichotoma (Hudson) Lamouroux (Plate VIII, Fig. 1).

Plant erect, 4–8 inches tall, flat, of dichotomous branches 3 cells thick, 3–8 mm. wide, and each with a prominent apical cell. Tetraspores, oogonia, or antheridia produced on both surfaces in the upper parts of the plant, each on separate plants. Tetrasporangia produced continuously, gametes produced periodically, the period unknown for the Gulf of Mexico but probably like that at Beaufort, N.C.

Common on rocks near Fort Massachusetts.

Reference: Hoyt, 1917–18, p. 461.

Dictyota cervicornis Kützing ? (Plate VI, Fig. 8).

With the characters of *D. dichotoma* except that the branching is irregularly dichotomous and somewhat cervicorn with slender branches 1–3 mm. wide.

Specimens fitting this species more closely than *D. dichotoma* were found on rocks near Fort Massachusetts. More reliable characteristics are needed to separate *D. cervicornis* and *D. dichotoma;* a detailed study of the genus in Florida and the West Indies is much needed.

Reference: Taylor, 1928, p. 118.

Padina vickersiae Hoyt (Plate VI, Fig. 9; Plate VIII, Fig. 9).

Plant of erect, orbicular blades that often split with maturity, of 4 cell layers above and 6–8 cell layers below the middle. Margin rolled. Reproductive elements similar to *Dictyota dichotoma* though the gametangia are evidently not periodic.

One of the most abundant of the larger algae on the rocks near Fort Massachusetts. Occasional small plants on the buoys in Ship Island Pass.

Reference: Hoyt, 1917–18, p. 456.

ORDER FUCALES

Family Sargassaceae

Sargassum filipendula C. Agardh (Plate VIII, Fig. 7).

Plants 1–3 feet tall, attached to rocks, terete stems with numerous leaf-like appendages having a distinct midrib and cryptostomata in one or more rows on each side of the midrib, thin, linear-lanceolate; air bladders spherical. Receptacles in paniculate arrangement on an axillary branch, the oocysts extruded periodically in relation to tide level, the period not known for the Gulf of Mexico.

Abundant on rocks near Fort Massachusetts and on ballast rocks off the former quarantine station where best developed in 6–10 feet of water.

Reference: Hoyt, 1917–19, p. 452.

Sargassum fluitans Børgesen (Plate IX, Fig. 1).

Similar in general structure to *S. filipendula* but more spreading, never attached, strictly pelagic, lacking cryptostomata and without sexual reproduction. Leaves lanceolate with broad teeth.

Occasional and temporary in Mississippi Sound brought in by wind and tide currents from the open Gulf.

Reference: Taylor, 1928, p. 127.

Sargassum natans (Linnaeus) Meyen (Plate IX, Fig. 1).

Differing from *S. fluitans* in its narrow, linear leaves with slender teeth. Also strictly pelagic.

Occasional and temporary in Mississippi Sound brought in by wind and tide currents from the open Gulf. Ordinarily more common than *S. fluitans.*

Reference: Hoyt, 1917–18, p. 452.

RHODOPHYTA

ORDER BANGIALES

Family Bangiaceae

Erythrotrichia carnea (Dillwyn) J. Agardh (Plate VII, Figs. 1, 2, and 3).

Epiphytic, erect, unbranched filament a few mm. tall, the cells 12–18 microns in diameter, 12–20 microns long, attached by a colorless basal cell. Monospores produced by unequal and oblique division of a vegetative cell, the upper of which is the monosporangium.

Abundant on most of the larger algae, rocks near Fort Massachusetts.

Reference: Hoyt, 1917–18, p. 466.

Goniotrichum alsidii (Zanardini Howe (Plate VII, Fig. 4).

Epiphytic, erect, of slender branched filaments, 1–3 mm. tall, with thick sheaths; cells cylindrical or elliptical, 7–10 microns wide, 11–20 microns long.

Occasional on larger algae, rocks near Fort Massachusetts, and on buoys in Ship Island Pass.

Reference: Hoyt, 1917–18, p. 465.

ORDER NEMALIONALES

Family Chantransiaceae

Achrochaetium crassipes Børgesen (Plate VII, Fig, 8).

Erect or sprawling, epiphytic, filamentous, uniseriate, attached by a single basal cell, the plant only about 60 microns tall, of one or two main filaments which are sparingly branched. Cells more or less isodiametric, 5–7 microns, the terminal cell often with a colorless hair. Monosporangia lateral, sessile, 5–6 by 6–8 microns.

On *Polysiphonia subtilissima* and other filamentous algae from the sides of the sunken iron barge near Fort Massachusetts.

Reference: Børgesen, 1913–20, p. 20.

Achrochaetium seriatum Børgesen (Plate VII, Fig. 5).

Erect, branched, filamentous, uniseriate, epiphytic, the basal attachment of irregular, creeping filaments, the erect filaments to 2 mm. tall, branched, 8–10 microns in diameter below, 6–7 microns in diameter above, cells 2–3 diameters long. Chromatophore parietal with one prominent pyrenoid. Monosporangia when mature about 10.5 by 15 microns in Mississippi specimens, sessile and secund on the upper side of branches or sometimes with a stalk cell.

Abundant on all the larger algae of all the Ship Island stations and on *Thalassia*. Forming a conspicuous fuzz.

Reference: Børgesen, 1913–20, p. 32.

PLATE VII

FIGS. 1, 2, 3. *Erythrotrichia carnea*, two filaments, and cells showing chromatophore and monospore formation. X 350, X 425, X 1300

4. *Goniotrichum alsidii*, upper part of plant. X 175

5. *Achrochaetium seriatum*, part of an erect branch arising from a basal filament. X 275

6. *Gracilaria foliifera*, cross section of a branch with two young tetrasporangia. X 450

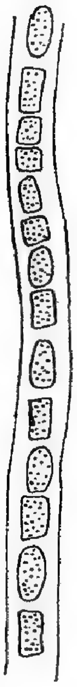
7. *Gelidium corneum*, branch from a tetrasporic plant. X 50

8. *Achrochaetium crassipes*, habit of plant. X 1000

9. *Gymnogongrus tenuis*, habit of plant. X 1

10. *Chondria leptacremon*, portion of a main axis with branch. X 35

(Figures 7 and 10 drawn by Joanna Woodson Parrish.)



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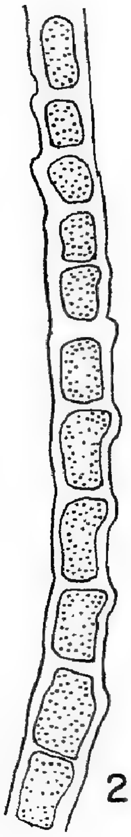

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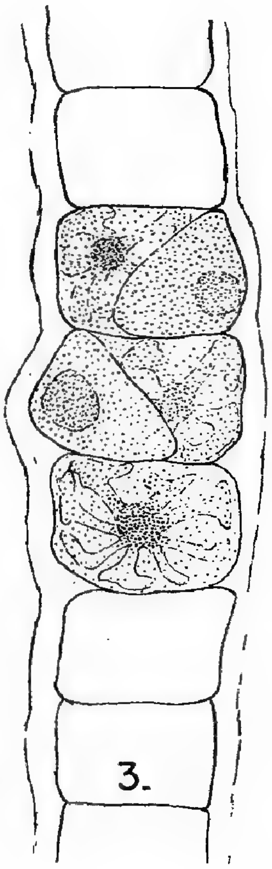

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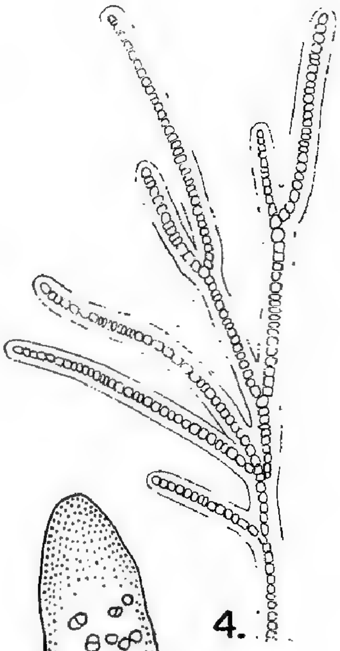

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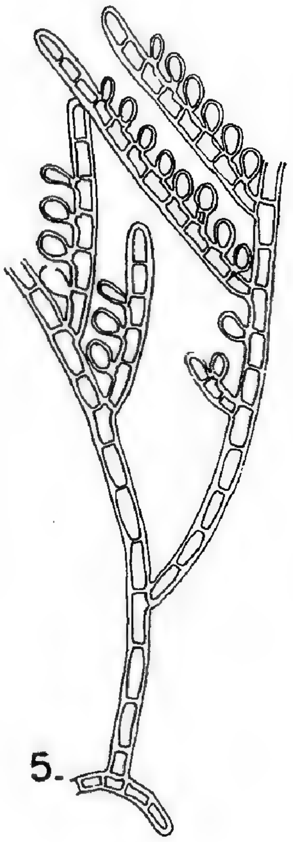

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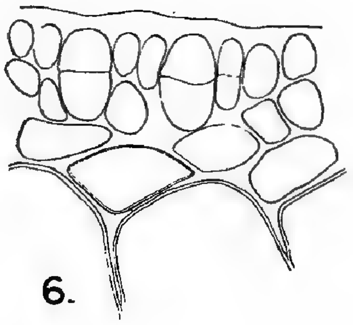

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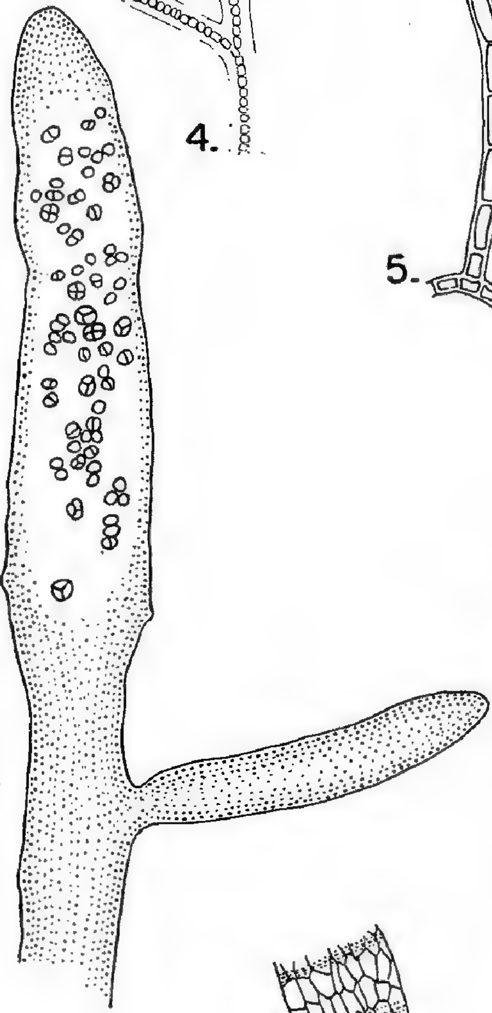

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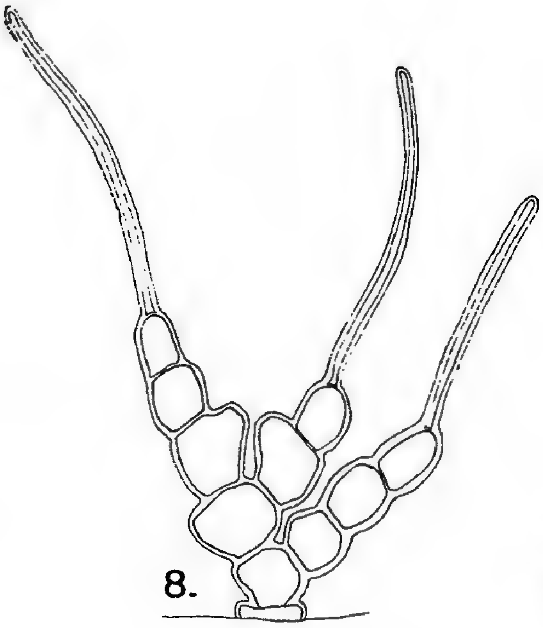

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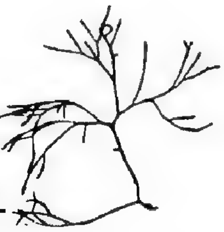

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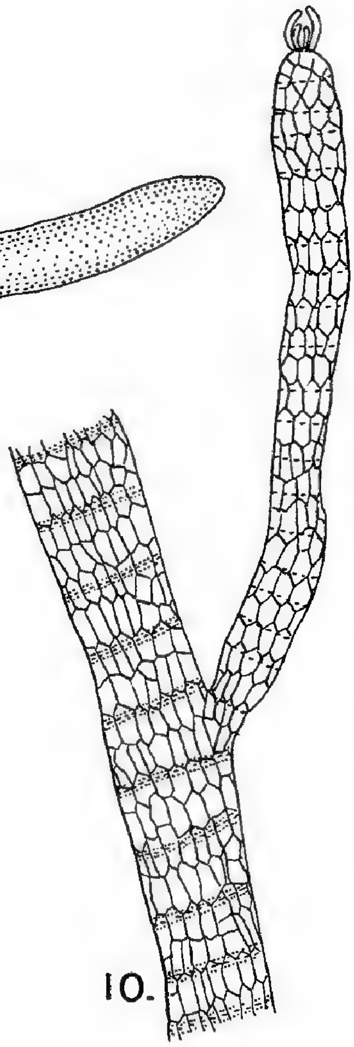

10.

ORDER GELIDIALES

Family Gelidiaceae

Gelidium corneum (Hudson) Lamouroux (*G. coerulescens* Kützing, *sensu* Hoyt, 1920.) (Plate VII, Fig. 7).

Plant erect, the branches flattened, 1–2 cm. tall, arising from a filiform creeping base, the erect parts densely branched, dark olive or purplish black, wiry, firmly attached.

Intertidal on the north wall of Fort Massachusetts and nearby rocks; on oyster shells from a submerged wreck off Ship Island light. Abundant.

Reference: Hoyt, 1917–18, p. 475 (as *G. coerulescens*).

Gelidium crinale (Turner) J. Agardh

Plants 2–7 cm. tall (or more at some stations), the branches terete, dark purplish brown, otherwise similar to *G. corneum.*

On the north wall of Fort Massachusetts and nearby rocks, Ship Island.

Reference: Hoyt, 1917–18, p. 475.

ORDER CRYPTONEMIALES

Family Corallinaceae

Fosliella farinosa (Lamouroux) Howe

Plants forming small, thin, flat, calcified, more or less rounded disks, 1–5 mm. in diameter, one cell thick in the vegetative parts, with colorless swollen cells at intervals. Conceptacles raised, hemispherical, with a single pore. Plants rose pink or white.

Abundant on leaves of *Thalassia* along the sound side of Ship Island and on larger algae around Fort Massachusetts.

Reference: Taylor, 1942, p. 91.

Fosliella lejolisii (Rosanoff) Howe

Similar to *F. farinosa* but lacking the colorless swollen cells scattered among the vegetative cells of the plant, and producing smaller disks on the average.

On the basal leaves of *Sargassum filipendula* from rocks near Fort Massachusetts. Evidently the less common of the two species.

Reference: Taylor, 1942, p. 91.

Family Grateloupiaceae

Grateloupia filicina (Wulfen) C. Agardh.

Plant bushy, branched, the branches somewhat flattened, greenish or purplish green in color, Mississippi specimens mostly 1–3 inches tall. Structurally composed of fila-

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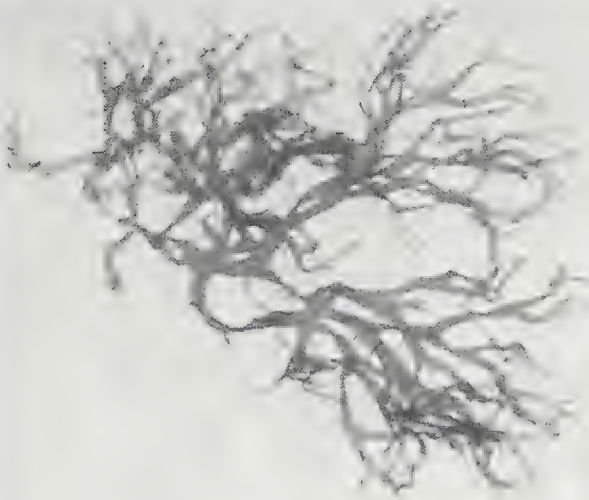
PLATE VIII

FIG. 1. *Dictyota dichotoma,* photograph of herbarium specimen. X ½
2. *Agardhiella tenera,* photograph of herbarium specimen. X ¼
3. *Spyridia filamentosa,* photograph of herbarium specimen. X 1
4. *Hypnea musciformis,* photograph of herbarium specimen. X 1
5. *Gracilaria foliifera,* photograph of herbarium specimen of small plant. X ½
6. *Bostrichia radicans,* photomicrograph of a portion of a plant with tetrasporic stichidia. X 35
7. *Sargassum filipendula,* photograph of herbarium specimen. X ¼
8. *Caloglossa leprieurii,* photomicrograph of a branch. X 11
9. *Padina vickersiae,* photograph of herbarium specimen. X ¼



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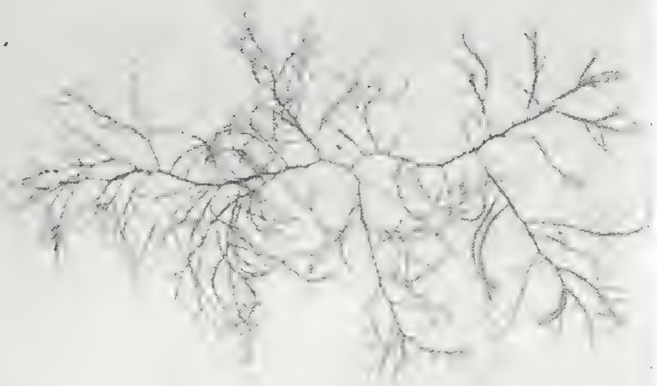

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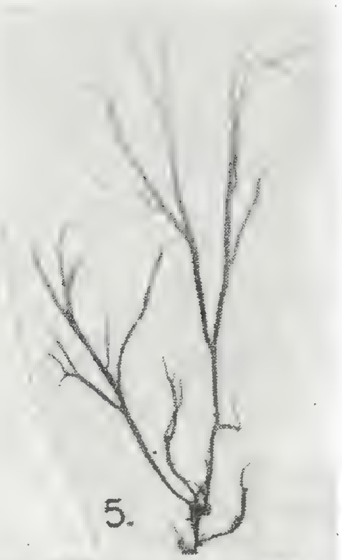

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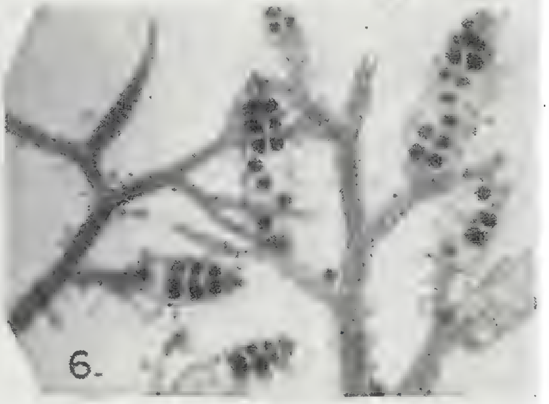

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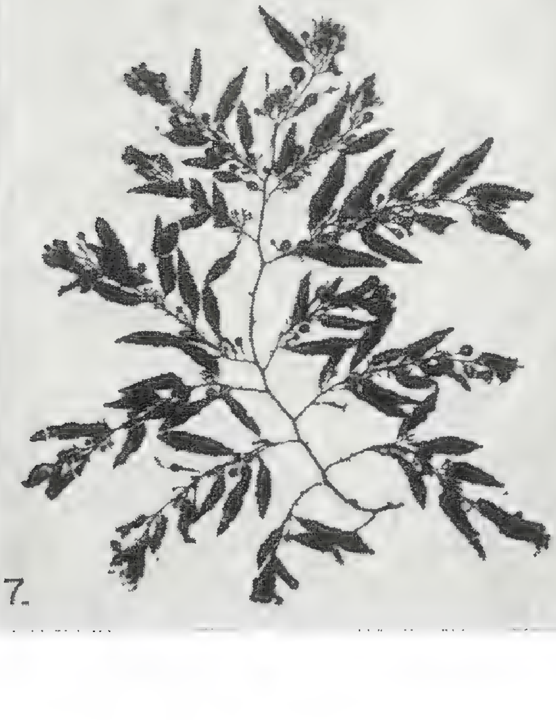

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ments, the central portion of rather loose, anastomosing filaments, those in the outer part compact and parallel. Tetraspores cruciate, scattered; cystocarps immersed, scattered.

Occasional small plants on the rocks near Fort Massachusetts. This species is easily confused with *Gracilaria* or *Agardhiella* in the field.

Reference: Hoyt, 1917–18, p. 521.

ORDER GIGARTINALES

Family Gigartinaceae

Gymnogongrus tenuis J. Agardh (Plate VII, Fig. 9).

Plants 2–4 cm. tall (Mississippi specimens), the main branching dichotomous with much irregular branching, the branches about 1 mm. wide, somewhat flattened, tough and wiry, greenish or brownish purple.

Abundant on nearby rocks and the north wall of Fort Massachusetts, intertidal, mixed with *Gelidium.*

Reference: Børgesen, 1913–20, p. 357.

Family Solieriaceae

Agardhiella tenera (J. Agardh) Schmitz (Plate VIII, Fig. 2).

Plants bushy, branched, to 1 foot tall or more, the branches mostly 2–4 mm. in diameter, terete, hollow in the center with loose, anastomosing filaments, these surrounded by two or three layers of parenchymatous cells and a small-celled epidermis. Tetraspores zonate, scattered at the surface. Cystocarps immersed, slightly protruding.

A single small plant was found on the rock breakwater near Fort Massachusetts in July. *Agardhiella* is a plant of winter and spring in the southern part of its range and is probably abundant around the fort from January to May. The more slender forms are easily mistaken for *Gracilaria.*

References: Børgesen, 1913–20, p. 361; Hoyt, 1917–18, p. 479.

Family Hypneaceae

Hypnea musciformis (Wulfen) Lamouroux (Plate VIII, Fig. 4).

Plants densely branched, 6–18 inches tall, olive green or purplish green, the branches terete, the ultimate branches short and spine-like. Longer branches often with a thickened, recurved tip. Tetraspores produced in swollen bands on the ultimate branches; cystocarps mainly external on small branches. The species is extremely variable in general appearance.

Evidently the most abundant alga on the rock breakwater below low tide during the summer months, becoming steadily more abundant until mid-November.

Reference: Hoyt, 1917–18, p. 485.

Family Gracilariaceae

Gracilaria foliifera (Forsskal) Børgesen (Plate VII, Fig. 6; Plate VIII, Fig. 5).

Plants moderately branched, 6–18 inches tall, green or purplish green, the branches terete to somewhat flattened, often forked in the upper parts, without spine-like branches or hooked tips. Tetraspores scattered, cruciate; cystocarps mainly external, on the main branches as well as the smaller branches.

Common on rocks of the breakwater near Fort Massachusetts, reaching its greatest abundance in October or November.

References: Hoyt, 1917–18, p. 484, as var. *angustissima* Harvey.

ORDER CERAMIALES

Family Ceramiaceae

Ceraminm fastigiatum (Roth) Harvey?

Filamentous, monosiphonous, corticated at the nodes only with a band of small cells, filaments long, sparingly branched, not dichotomous, rarely with forcipate tips, 40–50 microns in diameter at the nodes which are only slightly swollen. Internodes generally 40–90 microns long, though some are longer. Nodal cortication mainly of one large and one small row of cells, occasionally with additional small cells. Basal creeping filaments with rhizoids often have but a single row of 4 corticating cells at the nodes.

The most common alga on large oyster shells from the submerged wreck in Mississippi Sound off Ship Island lighthouse. The above description applies to Mississippi specimens only. Typical *C. fastigiatum* is dichotomous with forcipate tips, even-topped. The growth and branching habit of the Mississippi material suggests *C. deslongchampsii Chauvin* but the nodal cortication is quite different. It seems to resemble *C. cimbricum* H. Petersen, but in the absence of authentic material for comparison, it does not seem wise to assign it to this species, which has never been reported in American waters, although *C. strictum* (Kützing) Greville and Harvey is closely related.

References: Taylor, 1937, p. 333; Rosenvinge, 1923–24, p. 378.

Spyridia filamentosa (Wulfen) Harvey (Plate VIII, Fig. 3).

Plants slender, terete, 4–20 cm. tall, the main axes about 1 mm. in diameter and tapering upwards. Branches with alternate bands of short and longer cortical cells which taper to points at both ends. Upper ends of the branches bearing numerous, hair-like deciduous, determinate branches which are monosiphonous and corticated at the nodes like *Ceramium* and with pointed apical cells. Longer branches sometimes with a swollen, recurved tip.

Occasional, usually on larger algae, rock breakwater near Fort Massachusetts.

References: Hoyt, 1917–18, p. 512; Taylor, 1942, p. 124.

Family Delesseriaceae

Caloglossa leprieurii (Montagne) J. Agardh (Plate VIII, Fig. 8).

Plants forming flat, dichotomously branching blades, violet in color, lanceolate, prostrate, the segments 1–2 mm. wide, 3–5 mm. long, usually associated with *Bostrichia*, characteristic of brackish water and salt marshes.

Common in Mississippi Sound at the bases of *Spartina alterniflora* in salt marshes mixed with *Bostrichia radicans*, and elsewhere high in the intertidal zone, especially where shaded.

References: Taylor, 1928, p. 162; 1937, p. 345.

Family Rhodomelaceae

Bostrichia radicans Montagne (*B. rivularis* Harvey) (Plate VIII, Fig. 6).

Plant usually creeping or sprawling, the branching distichous and alternate, the larger branches bearing two opposite rows of short branches which may terminate in a monsiphonous filament. Pericentral cells 6–8 in the principal branches, divided once longitudinally thus half as long as the central cells; uncorticated. Plants restricted to the upper intertidal zone, abundant on the base of salt marsh grasses.

Widely distributed in Mississippi Sound on pier pilings, in salt marshes, on the north wall of Fort Massachusetts where it is the highest macroscopic alga.

References: Taylor, 1928, p. 167 (as *Amphibia rivularis*) ; Hoyt, 1917–18, p. 507, as *B. rivularis;* Post, 1955; Taylor, 1954, p. 106.

Bostrichia tenella (Vahl) J. Agardh

Similar to *B. radicans* except that the main axes become corticated with 3–4 layers of pericentral cells and the branchlets bear long, monosiphonous tips.

At the base of stems of *Spartina,* intertidal zone, salt marsh on Deer Island, Mississippi Sound.

References: Taylor, 1928, p. 167 (as *Amphibia tenella*) ; Post, 1955.

Chondria leptacremon (Melvill) DeToni (Plate VII, Fig. 10).

Plants creeping, with sprawling, more or less erect parts, usually epiphytic, sparingly branched, the main axes 300–350 microns in diameter. Branches constricted at the base, truncate at the apex with the growing point sunken in an apical pit with trichoblasts. Pericentral cells with convex thickenings of the upper endwalls which show through the cortex as dark lines (resembling *Champia* under low magnification), the pericentral cells 225–250 microns long in the main axes.

Occasional on other algae and easily overlooked, rock breakwater near Fort Massachusetts; buoys in Ship Island Pass.

Reference: Howe, 1920, p. 568.

Herposiphonia secunda (C. Agardh) Ambronn

Plants filamentous, polysiphonous, with creeping main axis 100–130 microns in diameter, giving rise to erect, unbranched, determinate branches 60–70 microns in diameter, 7–8 pericentral siphons, apices with trichoblasts.

A component of the quarter-inch high turf on the sides of a sunken iron barge near Fort Massachusetts, also on nearby rocks and buoys in Ship Island Pass.

References: Børgesen, 1913–20, p. 469; Taylor, 1928, p. 176.

Polysiphonia howei Hollenberg

Plants filamentous, polysiphonous, with a creeping main axis 100–170 microns in diameter, the segments isodiametric or shorter than broad, attached by numerous unicellular rhizoids. Pericentral cells 10–12. Erect branches 70–150 microns in diameter, unbranched or with a few branches; apices with trichoblasts.

Occasional on rocks of the breakwater, Fort Massachusetts, and on buoys in Ship Island Pass. Since all material examined was sterile, the determination is not certain.

Reference: Taylor, 1954, p. 302.

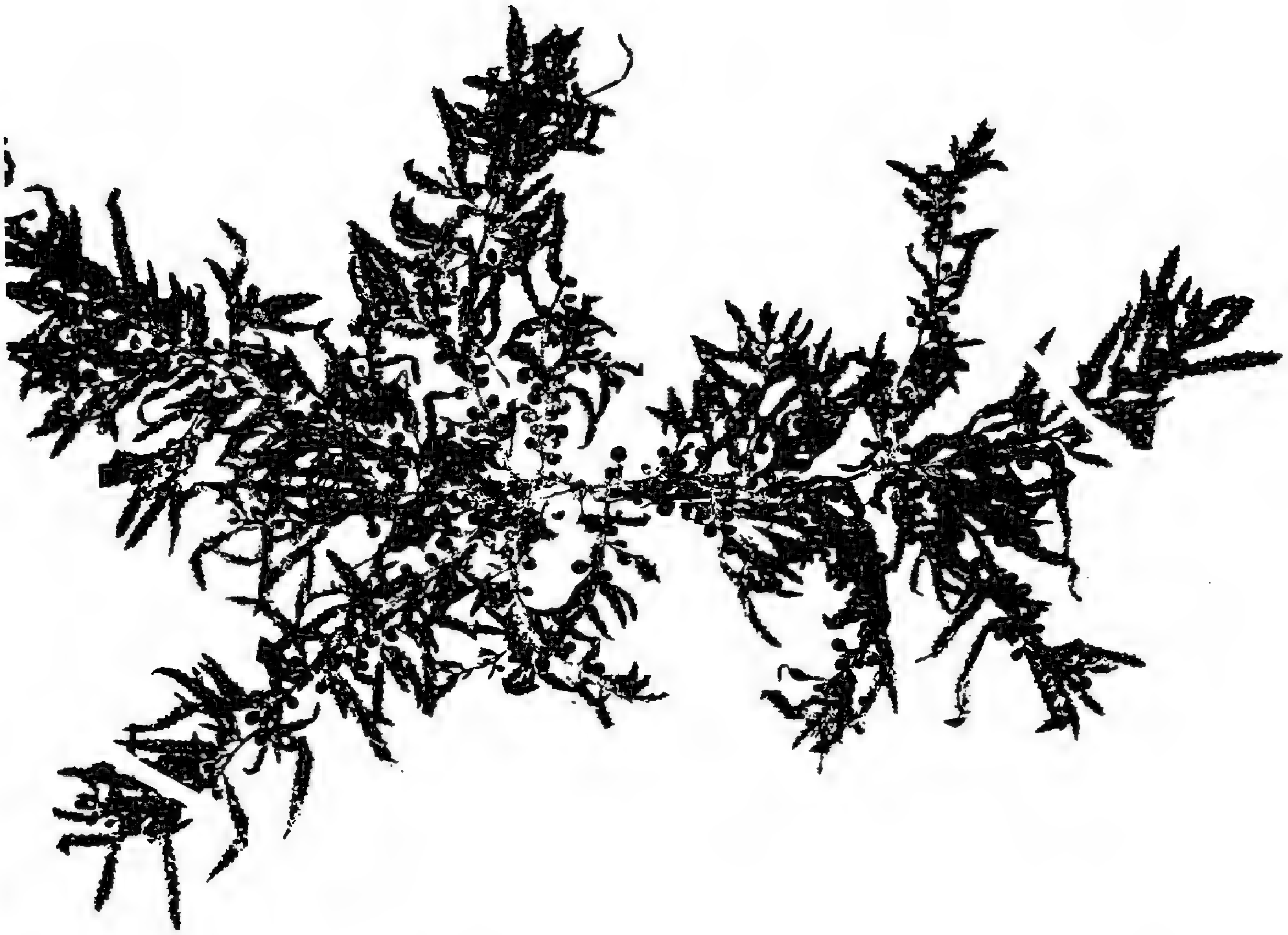
Polysiphonia subtilissima Montagne

Plants filamentous, polysiphonous, erect but with decumbent filaments, 4 pericentral cells, the segments as long as wide or shorter than wide in the main filaments, 1.5 to 3

PLATE IX

FIG. 1. *Sargassum fluitans,* photograph of herbarium specimen. X ¼

2. *Sargassum natans,* photograph of herbarium specimen. X ¼



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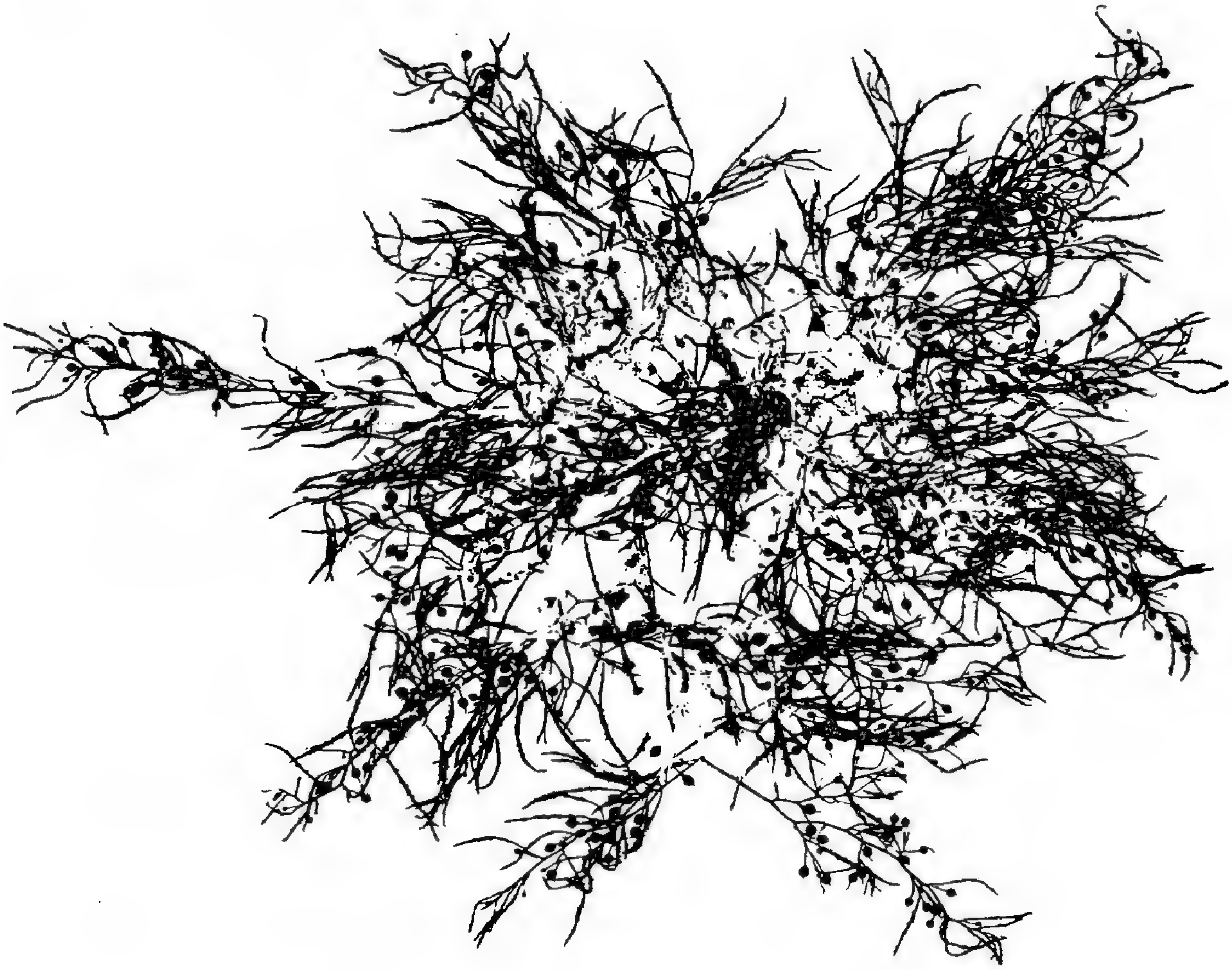

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diameters long in the upper parts. Tips of branches without trichoblasts, plants blackish purple. Erect filaments to 90 microns in diameter.

Common as part of a low turf on the sides of a sunken iron barge near Fort Massachusetts. Previously collected near the mainland at Waveland by Drouet (Taylor, 1954).

Reference: Taylor, 1928, p. 185.

Polysiphonia variegata (C. Agardh) Zanardini

Similar to *P. subtilissima* but with 6 pericentral cells and trichoblasts, the main axes to 350 microns or more in diameter, the branches wide-angled, plants dark in color.

Common on the sides of a sunken iron barge near Fort Massachusetts.

References: Hoyt, 1917–18, p. 503 (as *P. denudata*) ; Taylor, 1937, p. 370.

Lophosiphonia sacchoriza Collins and Hervey ? (Plate VI, Figs. 10 and 11).

Plants filamentous, polysiphonous with 4 pericentral cells, the main axes creeping and giving rise to erect, determinate (?) branches. Basal filaments mostly 50–60 microns in diameter, the erect branches about 50 microns in diameter at the base, tapering upwards to about 30 microns. Segments 1–2 diameters long, trichoblasts well-developed. Erect branches usually with 1–3 small branches, these sometimes branched again.

Creeping on old oyster shells from a submerged wreck off Ship Island lighthouse, Mississippi Sound.

While this material agrees in many respects with *L. sacchoriza,* the rhizoids seem to be less expanded than in the Bermuda type material, which was epiphytic on *Codium.* If the species grows on a substratum other than *Codium,* it would not be expected to develop rhizoids of the same size and shape. In the Mississippi plant, the rhizoids are generally saccate if they penetrate a soft substratum, but are coralloid if they encounter a solid surface (Plate VI, Fig. 10). Other collections evidently identical with that from Mississippi have been secured by the senior author off Wakulla County, Florida, and on *Thalassia* at Bimini, Bahamas, also without the extremely expanded rhizoids.

Because of the exogenous origin of the branches and lack of a distinct dorsiventral organization in this plant, it probably should be referred to the genus *Polysiphonia.* Until the recent collections are compared with the Bermuda type material, however, there may be doubt that the two are the same .

Reference: Collins and Hervey, 1917, p. 127.

Key to the Summer Marine Algae of Mississippi Sound

The following key has been included in order to provide a better means than at present available for students of the Gulf Coast Research Laboratory to identify the summer marine algae of Mississippi Sound. At the same time, the inclusion of the key implies that virtually all the algae to be expected are included. Such is probably not the case. In an effort to avoid incorrect identifications arising from the collection of material not in the key, more characters have been used than are necessary to separate the species included, especially in places where a species not yet recorded for Mississippi Sound, but suspected to be present, would key out.

The key should be used with caution at other localities, even as close as the Chandeleur Islands.

CYANOPHYTA

1 Plants without chromatophores, the pigment in solution or in colloidal dispersion in the cytoplasm; no organized nucleus; microscopic filaments or groups of cells green to bluegreen in color; no storage of starch (Phylum *Cyanophyta*, the bluegreen algae) 2

1 Plants with chromatophores and an organized nucleus 29

2 Plants unicellular, the cells gregarious or colonial; not basally attached to a substratum (except by the sheath); dividing into cells of equal size; cells spherical before division and distributed through a gelatinous matrix (Genus *Anacystis*) 4

2 Plants basally attached to a substratum if unicellular or colonial; or distinctly filamentous 3

3 Plants unicellular or multicellular (often boring into shells or limestone within which they may be filamentous); solitary cells or groups basally attached to a substratum; cell division unequal; endospores produced (Fam. *Chamaesiphonaceae*, Genus *Entophysalis*) 6

3 Distinctly filamentous, attached or unattached 7

4 Cells 0.5 to 2 microns in diameter .... *Anacystis marina*

4 Cells exceeding 5 microns in diameter 5

5 Cells mostly 6–12 microns in diameter .... *Anacystis aeruginosa*

5 Cells 12–50 microns in diameter .... *Anacystis dimidiata*

6 On wood, rocks or shells; boring into shells or limestone within which the plant is filamentous .... *Entophysalis deusta*

6 On larger algae and live animals .... *Entophysalis conferta*

7 Filaments without a gelatinous sheath, unbranched, not long tapering (Sheaths are easily overlooked if they are confluent, and filaments sometimes move out of their sheaths) 8

7 Sheath present (may be difficult to see if sheaths are confluent) 12

8 Trichomes distinctly spiraled; without crosswalls 9

8 Trichomes not spiraled; crosswalls present 10

9 Turns of the spiral contiguous or nearly so .... *Spirulina subsalsa*

9 A loose spiral with 2.5 to 5 microns between the turns .... *Spirulina major*

10 Trichomes forming a fasciculate bundle in the plankton, bent, 7–16 microns diameter, nodes not constricted .... *Trichodesmium thiebautii*

10 Not typically planktonic 11

11 Trichomes 4.5 to 6.5 microns diameter, nodes not constricted, apex tapering, cells 2.5 to 4.2 microns long, the apical cell longer .... *Oscillatoria subuliformis*

11 Trichomes 7–11 microns diameter, nodes somewhat constricted, cells 3–6 microns long, transverse walls with refringent granules .... *Oscillatoria nigro-viridis*

12 Filaments without heterocysts 13

12 Filaments with heterocysts 26

13 Filaments long-tapering; plant mass of two layers, the lower of interwoven filaments, the upper of erect, unbranched, tapering filaments, 2–3 microns wide, cells shorter than wide, nodes constricted, hormogonia in series .... *Amphithrix violacea*

13 Filaments not long-tapering 14

14 Filaments unbranched 15

14 Filaments with false or true branches 23

15 Trichomes single within the sheath 16

15 Trichomes several to many within the sheath 22

16 Sheaths distinct, not diffluent 17

16 Sheaths becoming diffluent, forming a gelatinous matrix (a condition easily interpreted as sheaths lacking) 21

17 Trichomes less than 2 microns wide, spirally wrapped around larger, filamentous algae .... *Lyngbya epiphytica*

17 Trichomes larger 18

18 Trichomes 2.5 to 6 microns diam., nodes not constricted cells 1.5 to 5.5 microns long .... *Lyngbya lutea*

18 Trichomes larger 19

19 Trichomes 5–12 microns wide, cells 2–3 microns long, nodes not constricted, apical cell with calyptra .... *Lyngbya semiplena*

19 Trichomes 8–25 microns diam., nodes not constricted 20

20 Apex of trichome not tapering; not capitate; apical cell rotund, without calyptra; cells 2–4 microns long .... *Lyngbya confervoides*

20 Apex of trichome slightly tapering, capitate; apical cell with slightly thickened outer membrane; cells 2.7 to 5.6 microns long, nodes slightly constricted .... *Lyngbya aestuarii*

21 Trichomes 1–2 microns diam., apex tapering, bent; cells 2.5 to 5 microns long, nodes slightly constricted .... *Phormidium tenue*

21 Trichomes 5 microns in diam., apex straight, gradually tapering; cells 4–10 microns long, nodes slightly constricted .... *Phormidium submembranaceum*

22 Trichomes 1.5 to 2 microns in diameter .... *Microcoleus tenerrimus*

22 Trichomes 2.5 to 6 microns in diameter .... *Microcoleus chthonoplastes*

23 Trichomes single within the sheath 24

23 Trichomes several within a sheath, 8–16 microns diam., cells 2.5 to 4.5 microns long, nodes not constricted, apex of trichome tapering, truncate .... *Hydrocoleum lyngbyaceum*

24 Trichomes 1 to 1.5 microns in diameter 25

24 Trichomes 4–6 microns diam., nodes constricted, cells 2–6 microns long; false branches, if present, solitary; filaments in erect tufts; apical cell with calyptra........ *Symploca atlantica*
25 Cells 2 to 2.5 microns long, nodes constricted, cytoplasm without granules .... *Plectonema nostocorum*
25 Cells 2–6 microns long, nodes not constricted, 2 refringent granules at the crosswalls; plants usually penetrating shells or limestone, but sometimes grow at the surface .... *Plectonema terebrans*
26 Filaments long-tapering and hair-tipped 27
26 Filaments not long-tapering to a hair, 6–7 microns diam., unbranched; gonidia 8 microns in diam., in a series .... *Nodularia harveyana*
27 Branches of 2 kinds, one cylindrical, the other tapering to a hair, 3.5 to 6 microns diam.; heterocysts lateral and terminal, swollen, spherical, 6–18 microns diam.; plants penetrating shells or limestone .... *Mastigocoleus testarum*
27 Branches all alike; plants not penetrating limestone 28
28 Heterocysts basal only; filaments 10–18 microns diam., to 1 mm. high, long tapering to a hair; trichomes 8–15 microns diameter........ *Calothrix confervicola*
28 Heterocysts basal and intercalary, filaments 12–40 microns diam., 1–2 mm. high; trichomes 8–15 microns diameter .... *Calothrix crustacea*

CHLOROPHYTA

29 Plants green; starch is stored (except *Vaucheria*); filamentous and monosiphonous, creeping or erect; a hollow tube with walls 1 cell thick; or a flat sheet Phylum *Chlorophyta* 30
29 Plants brown or red, or if green of different structure from the above 42
30 Erect, microscopic unbranched filaments 5–6 microns in diam. .... *Stichococcus marinus*
30 Plants otherwise 31
31 Plants without erect branches; microscopic creeping filaments or a flat plate of cells........ 32
31 Plants with erect parts 35
32 Filaments coenocytic, boring in shells or limestone, 4–5 microns in diam. with inflated parts to 40 microns .... *Ostreobium quekettii*
32 Plants divided into cells 33
33 Plant a flat plate or disk to 1 mm. in diam., of radiating cells; on other algae, stones or shells .... *Ulvella lens*
33 Plant composed of horizontal creeping filaments 34
34 Occasional cells of filament with erect zig-zag or spiral colorless hairs; cells mostly 9–15 microns diam. .... *Phaeophila floridearum*
34 No hairs; cells 3–6 microns wide, 1–6 diameters long .... *Entocladia viridis*
35 Plants of erect monosiphonous filaments attached at the base or forming a loose mass 36
35 Plants consisting of a hollow tube or a flat sheet 39
36 Filaments coenocytic, the lower parts usually embedded in soft mud........ *Vaucheria thuretii*
36 Filmanets with crosswalls 37
37 Abundantly branched 38
37 Rarely branched, the branches short and rhizoidal; filaments usually 15–30 microns wide .... *Rhizoclonium riparium*
38 Main filaments over 150 microns diam., usually a plant of wave-beaten localities .... *Cladophora fascicularis*
38 Main filaments less than 150 microns diam., ultimate branches often in pectinate series at tips of long branches; typically a plant of salt marshes as well as exposed localities .... *Cladophora gracilis*
39 Plant a hollow tube, often collapsed, the walls 1 cell thick 40
39 Plant a flat sheet two cells thick .... *Ulva lactuca*
40 Unbranched, the cells in longitudinal rows........ *Enteromorpha flexuosa*
40 At least sparingly branched from the base 41
41 Branching mostly from the base, the branches progressively larger upward for 1–5 mm. above the base .... *Enteromorpha lingulata*
41 Branching throughout, the branches terminating in a single series of cells; chromatrophores not filling the cells .... *Enteromorpha plumosa*
42 Plants brown, starch not stored (Phylum *Phaeophyta*) 43
42 Plants usually red, sometimes green; if green, of a different structure from #29 of this key 55

PHAEOPHYTA

43 Filamentous, monosiphonous or polysiphonous, erect 44
43 Not filamentous; plants larger 50
44 Polysiphonous, to 5 mm. tall; asexual reproduction by shield-shaped or triangular propagulae .... *Sphacelaria tribuloides*........
44 Monosiphonous (genus *Ectocarpus*) 45
45 Plant less than 2 mm. tall, epiphytic, of tangled, horizontal filaments giving rise to unbranched, erect filaments which bear elongate gametangia near their base...... *Ectocarpus elachistaeformis*
45 Plants taller 46
46 Gametangia ending in a long hair .... *Ectocarpus siliculosus*
46 Gametangia not hair-tipped 47

47 Gametangia long-tapering, 60–400 microns long, 20–40 microns in diam., apex rounded .... *Ectocarpus confervoides*
47 Gametangia shorter and more blunt 48
48 Gametangia mostly 10–17 microns diam., 60–150 microns long, often terminal on short branches, plants 5–7 cm. tall .... *Ectocarpus dasycarpus*
48 Gametangia usually over 17 microns diam., not terminal on short branches 49
49 Gametangia 15–20 microns in diam., 70–100 microns long; main filaments of plant 35–45 microns diam., the apex rounded .... *Ectocarpus mitchellae*
49 Gametangia 25–30 microns diam., 100–250 microns long; main filaments 20–22 microns in diam., plants 2–5 cm. tall .... *Ectocarpus duchassaignianus*
50 Branches dichotomous, flattened, 2–10 mm. wide 51
50 Branching not dichotomous 52
51 Branching irregularly dichotomous, somewhat cervicorn; branches 1–3 mm. wide .... *Dicyota cervicornis*
51 Branching more regularly dichotomous, the branches mostly 3–6 mm. wide .... *Docyota dichotoma*
52 Plant a flat, orbicular blade, often split, with rolled margin; 5–15 cm. high .... *Padina vickersiae*
52 Plant with terete stems bearing leaf-like appendages and spherical air bladder (Genus *Sargassum*) 53
53 Growing attached, leaves with cryptostomata, and bearing receptacles .... *Sargassum filipendula*
53 Always drifting, leaves without cryptostomata, receptacles not produced 54
54 Leaves linear with slender marginal teeth .... *Sargassum natans*
54 Leaves lanceolate, marginal teeth broad .... *Sargassum fluitans*

RHODOPHYTA

55 Plants in the form of calcified disks, 1–5 mm. in diameter, epiphytic 56
55 Plants not calcareous 57
56 With colorless swollen cells at intervals among the typical vegetative cells .... *Fosliella farinosa*
56 Without colorless swollen cells .... *Fosliella lejolisii*
57 Plants composed of flat, leaf-like segments 1–2 mm. wide with a mid-rib; associated with *Bostrichia* at the base of salt marsh grasses and elsewhere high in the intertidal zone .... *Caloglossa leprieurii*
57 Plants filamentous or parenchymatous 58
58 Plants filamentous, monosiphonous, uncorticated, erect, essentially microscopic, epiphytic 59
58 Plants corticated, at least at the nodes; or polysiphonous or parenchymatous; microscopic or larger 62
59 Filaments unbranched, 16–26 microns diam., usually less than 2 mm. tall; monospores formed by oblique division of vegetative cells .... *Erythrotrichia carnea*
59 Branched 60
60 Without protoplasmic connections between cells; cells shorter than wide or isodiametric; vegetative cells developing into monospores; protoplast red-violet; filaments 12–20 microns diam., sheaths thick; plants 2–5 mm. tall .... *Goniotrichum alsidii*
60 With protoplasmic connections between cells; attached by an enlarged basal cell or by a group of creeping filaments 61
61 Plant minute, less than 100 micorns tall, a single basal cell with 1–3 partially erect filaments, most ending in a long colorless hair .... *Achrochaetium crassipes*
61 Plant about 1 mm. tall, base of creeping filaments; erect filaments 8–10 microns diam., below; monosporangia in rows on upper sides of branches .... *Achrochaetium seriatum*
62 Plant monosiphonous, corticated at the nodes; filaments 40–50 microns diam., not dichotomous; usually 1 row of large and 1 row of small cortical cells at a node .... *Ceramium fastigiatum*
62 Plant polysiphonous, except the ultimate branches in some; or apparently not filamentous and larger 63
63 Not corticated, filamentous 64
63 Corticated if filamentous; or parenchymatous 69
64 With four pericentral siphons 65
64 With more than four pericentral siphons 66
65 Main filaments creeping, horizontal, 50–60 microns diam., producing sparingly branched erect filaments 30–60 microns diameter .... *Lophosiphonia sacchoriza*
65 Main filaments erect; no colorless hairs at apex of branches .... *Polysiphonia subtilissima*
66 Six pericentral siphons; main filaments erect .... *Polysiphonia variegata*
66 Six to many pericentral siphons; if only 6, the main filaments creeping, horizontal 67
67 Main filaments creeping and giving rise to more or less determinate, erect branches 68
67 Main filaments erect or sprawling with 6–8 pericentral cells; some branches with monosiphonous tips; high in the intertidal zone, usually in brackish water .... *Bostrichia radicans*
68 Erect branches unbranched, usually of 35–45 segments, 60–90 microns diam., creeping filaments 80–130 microns diam. .... *Herposiphonia secunda*

68 Erect branches occasionally branched .... *Polysiphonia howeii*
69 At base of salt marsh grasses or elsewhere high in the intertidal zone; plant dorsiventral in structure, olivaceous, many branches terminating in long, monosiphonous filaments .... *Bostrichia tenella*
69 Below low tide, or if intertidal rarely above the midtide line 70
70 Plants blackish or dark alive, wiry, firmly attached to rocks, usually less than 1 inch tall, the branches less than 1 mm. in diameter; low intertidal and below, except where shaded or splashed by surf 71
70 Plants otherwise 73
71 Branching dichotomous, the branches terete at the base, somewhat flattened above .... *Gymnogongrus tenuis*
71 Branching pinnate or irregular 72
72 Branches slender, terete .... *Gelidium crinale*
72 Branches in part distinctly flattened .... *Gelidium corneum*
73 Plant with monosiphonous ultimate branches of determinate growth, these corticated at the nodes like *Ceramium* .... *Spyridia filamentosa*
73 Plants without monosiphonous ultimate branches 74
74 Central portion of branches with anastomosing filaments (seen in cross section) 75
74 Central portion of branches with parenchymatous cells 76
75 Branches flattened, tetraspores cruciate .... *Grateloupia filicina*
75 Branches terete, tetraspores zonate .... *Agardhiella tenera*
76 Plant in part creeping, less than 1 inch tall; apices of branches with a tuft of colorless hairs .... *Chondria leptacremon*
76 Plants larger, erect, without terminal hair tufts 77
77 Branches terete, sometimes ending in hooked tips; plant with numerous small branches, the tetraspores borne in a zone on ultimate branches .... *Hypnea musciformis*
77 Branches somewhat flattened, without hooked tips or numerous small branches; tetraspores scattered .... *Gracilaria foliifera*

GLOSSARY

akinete—a sexual reproductive cell formed by the thickening of the wall of a vegetative cell.
anastomosing—forming an irregular network.
antheridium—structure producing male gametes or sperm.
apical—at the apex or tip.
arborescent—branched like a tree.
axillary—arising in the angle of a stem and leaf or stem and branch.
calyptra—thickening of the outer wall of the apical cell.
capitate—in the bluegreen algae, the termination of a filament in a more or less globose head.
cervicorn—branching one-sided, similar to the horns of a deer.
chromatophore—pigment-containing body of a plant cell.
coenocytic—not divided into cells; a filament without crosswalls.
confluent—fused into a gelatinous mass (with ref. to sheaths) so that the boundaries are not distinguishable.
corticated—having a cortex; in the *Rhodomelaceae,* cells covering the pericentral siphons which arise as a result of further cell division thus not directly produced by the growing tip.
cruciate—tetraspores produced by division of the mother cells forming walls at right angles to each other; grouped around a common center.
cryptostoma—in the brown algae (*Sargassum,* for example) a small cavity in the leaves which bear hairs only.
cystocarp—a mass of carpospores and accessory structures produced on female plants of the red algae arising as a result of fertilization of an egg cell.
deciduous—falling off naturally.
determinate—not growing beyond a certain size.
dichotomous—branching by forking into two parts of equal size.
diffluent—said of the sheaths of bluegreen algae which fuse and form a common gelatinous matrix.
dorsiventral—having unlike surfaces as upper and lower.
endophytic—growing within the tissue or sheath of another plant.
epiphytic—growing upon another plant.
false branching—in the bluegreen algae where a trichome pushes its way through the side of the sheath.
fasciculate—a close cluster of parallel filaments, stems, or branches.
filament—a plant or a branch composed of a single row of cells.
filamentous—composed of one or more filaments.
flagelliform—resembling a slender thread.
gametangium—a cell producing gametes.
gonidium—an asexual reproductive cell.
heterocyst—in the bluegreen algae, an enlarged transparent cell, often with a thick wall.
hormogone, hormogonium—in the bluegreens, a multicellular portion of a filament which becomes separate, with rounded ends, and serves to distribute the species.

intercalary—located somewhere between the base and apex.
lamellose—having visible layers.
lanceolate—narrow but tapering at each end.
linear—narrow, several times longer than wide, with a rather abrupt taper.
monosiphonous—consisting of a single row of cells.
monospore—a spore formed from the entire contents of a cell or monosporangium.
node—in a monosiphonous filament, the endwalls of two adjacent cells.
olivaceous—a greenish-brown color.
oocyst—egg cell and surrounding gelatinous material.
oogonium—single-celled female organ bearing one or more egg cells.
orbicular—flat with a circular outline.
parenchymatous—tissue composed of thin-walled cells rectangular or polyhedral in shape; not filamentous in structure.
parietal—just inside the wall; not in the center.
pectinate—producing a series of branches from one side like the teeth of a comb.
penicillate—brush-like; fastigiate.
pericentral—filaments (or cells) forming a ring around a central filament, all of which were laid down by the growing tip.
pinnate—with branches along opposite sides of a stem, something like a feather.
polysiphonous—composed of a group of continuous vertical filaments, as, for example, with a central siphon surrounded by four pericentrals.
propagulum—a multicellular body formed from a vegetative part of the plant which breaks loose and serves to reproduce the species.
pyrenoid—a small rounded colorless body in a chromatophore serving as a center of starch accumulation.
receptacle—in *Sargassum* (and related genera), a small, specialized branch borne in leaf axils which produces cavities or conceptacles in which eggs or sperms are produced.
rhizoid—a one- to many-celled filmanet serving as an organ of attachment.
secund—bearing appendages in a row along one side of a branch.
sessile—attached without a stalk.
sheath—the gelatinous coating covering cells or filaments, especially among the bluegreen algae.
subulate—long, slender, and pointed.
terete—cylindrical; round in cross-section.
tetraspore—one of four spores formed in a tetrasporangium.
trichoblast—a branched or unbranched colorless hair, usually deciduous and usually produced at the growing tip.
trichome—in the bluegreen algae, the row of cells exclusive of the sheath.
truncate—more or less squared off at the end.
uniseriate—composed of a single row of cells.
zonate—a formation of tetraspores in which they are one on top of the other, or in a single row of four.

Summary

Twenty-seven *Cyanophyta*, 12 *Chlorophyta*, 1 member of the *Chrysophyta*, 13 *Phaeophyta*, and 24 *Rhodophyta*, totaling 77 species, were collected in Mississippi Sound, the majority from the inside of Ship Island, across the sound from Biloxi and Gulfport. The north wall and bordering rocks of Fort Massachusetts, a nearby breakwater, and a submerged wreck were the most productive collecting stations.

The salinity of the water from which the majority of these algae came ranged from 21 to 32‰ during the summer months of 1955, and the water temperature ranged from 28 to 32° C.

Sixty-six of the 77 species are here newly reported for the coast of Mississippi. In addition, 4 genera and species of marine monocotyledonous plants were observed in abundance along the sound side of Ship Island and other islands bordering Mississippi Sound.

LITERATURE CITED

Børgesen, F. 1913. Marine algae of the Danish West Indies. I. Chlorophyceae, Phaeophyceae. *Dansk Bot. Ark.*, 1(4) : 1–158.

——————. 1914. *Ibid.* 2(2) : 1–66.

——————. 1915–20. Marine algae of the Danish West Indies. II. Rhodophyceae. *Dansk Bot. Ark.*, 3: 1–504.

Bornet, E., and C. Flahault. 1886. Revision des Nostocacees Heterocystees. I. *Ann. Sci. Nat.*, ser. 7, 3: 323–381.

————. 1887. *Ibid.* III., 5: 51–129.

————. 1888. *Ibid.* IV., 7: 177–262.

Collins, F. S. 1909. The green algae of North America. Tufts Coll. Stud. (Sci. Ser.), 2(3): 79–480.

Collins, F. S. and A. B. Hervey. 1917. The algae of Bermuda. *Proc. Amer. Acad. Arts Sci.*, 53: 3–195.

De Toni, G. B. 1889. Sylloge algarum omnium hucusque cognitarum. Vol. I (Sylloge Chlorophycearum), Parts 1 and 2. I–CXXXIX, 1–1315.

Drouet, F., and W. A. Daily. 1956. Revision of the cocoid Myxophyceae. Butler U. Bot. Stud., 12: 1–218.

Fan, K. C. 1956. Revision of *Calothrix* Agardh. Rev. Algologique n.s., 3(3): 1954–178.

Gomont, M. A. 1892. Monographie des Oscillariees. Ann. Sci. Nat. ser. 7, 15: 263–368; 16; 91–264.

Hansgirg, A. 1887. Physiologische und Algologische Studien. Leipzig.

Howe, M. A. 1920. Algae in N. L. Britton and C. F. Millspaugh, *The Bahama Flora.* vii+695 pp. New York. pp. 553–626.

Hoyt, W. D. 1917–18. Marine algae of Beaufort, N. C., and adjacent regions. Bull. U. S. Bur. Fish., 36: 367–556 + 36 plates.

Huber, J. 1892. Contributions a la connaissance des Chaetophorees epiphytes et endophytes et de leure affinities. Ann. Sci. Nat., ser. 7, Botanique, 16: 265–353.

Humm, H. J. 1956. Sea grasses of the northern Gulf coast. Bull. Mar. Sci. Gulf & Carib., 6: 305–308.

International Code of Botanical Nomenclature. 1956. Utrecht.

Newton, Lily. 1931. A Handbook of the British Seaweeds. London, Brit. Museum, pp. 1–478.

Pew, Shelba G. 1941. A summer phase of *Enteromorpha lingulata* J. Agardh at Beaufort, N. C. Unpubl. master's thesis, Duke Univ.

Post, Erica. 1955. Weitere Daten zur Verbreitung des Bostrychietum. V. Ber. Deut. Bot. Ges., 68: 205–216.

Rosenvinge, L. K. 1923–24. The marine algae of Denmark, III. K. Danske Vidensk. Selsk. ser. 7, 7(3): 287–486.

Rosenvinge, L. K. and S. Lund. 1941. The marine algae of Denmark, Vol. II, *Phaeophyceae.* K. Dans. Vidensk. Selsk., Biol. Skrifter 1(4): 1–79.

Taylor, W. R. 1928. The marine algae of Florida with special reference to the Dry Tortugas. Publ. Carneg. Inst., 379; Papers from the Tortugas Lab., 25: 1–219.

————. 1937. Marine Algae of the Northeastern Coast of North America. Ann Arbor, U. of Mich. Press, pp. 1–405, 59 plates.

————. 1942. Caribbean marine algae of the Allan Hancock Expedition, 1939. Rept. Allan Hancock Atlant. Exped., 2:1–193, 20 plates.

————. 1945. Pacific marine algae of the Allan Hancock expeditions to the Galapagos Islands. Allan Hancock Pacif. Exped., 12: 1–528. 100 plates.

————. 1954. Distribution of marine algae in the Gulf of Mexico. Pap. Mich. Acad. Sci., Arts, Lett., 39: 85–109.

Tilden, Josephine E. 1910. The Myxophyceae of North America and adjacent regions. Minn. Algae, Vol. I, Minneapolis, U. of Minn. Press, pp. 1–328, 20 plates.

The Effects of Suspended Materials on the Reproductive Rate of *Daphnia magna*[1]

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Introduction

The factors responsible for differences in zooplankton populations from one aquatic habitat to another are not always obvious. Marked variations in temperatures, pH, depth, and turbidity, for example, are known to limit and define the distribution of planktonic animals (Ruttner, 1953). Other influences, however, which might restrict the distribution of species and the habitability of aquatic environments may be more subtle. Experimental ecology has in recent years demonstrated several of these important "subtle" factors. For example, species competition (Frank, 1952) and the production of zooplankton inhibitors by algae (Ryther, 1954) are two influences which might be overlooked in field observation and sampling, but which are important to the survival of plankters and the balance of the aquatic community.

In spite of large and conspicuous variations, turbidity as a factor affecting organisms is little understood. The actions of turbidity as an environmental influence may at times be obvious, but at other times may be quite inconspicuous. Many descriptive observations have been made on turbid waters and many of the effects of turbidity have been suggested. Ellis (1936) indicated that the presence of erosional silt particles produced a "skew lag" in temperature changes in turbid water. Welch (1952) noted that turbid waters were somewhat warmer than clear waters. Doan (1942) suggested that there was a migration of zooplankton toward the surface in turbid water.

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Some deleterious effects were observed. Chandler (1942b) noted that high turbidities prior to a phytoplankton bloom decreased the length and strength of the bloom. It was also noted by Ellis (1936) that the addition of erosional silt caused a decrease in plankton due to decreased light penetration, accompanied by a decrease in available electrolytes. Meyer and Heritage (1941) demonstrated a significant change in the depth of the compensation point of *Ceratophyllum demersum* in response to a decrease in light brought about by increased turbidities. A decrease in fish production due to erosional silt was suggested by Moore (1937), who also claimed that bottom dwellers diminished in highly silted areas.

On the other hand, Wallen (1951) did not note any direct deleterious effects to fishes experimentally except at extremely high (greater than 100,000 ppm) concentration of a montmorillonoid clay. A positive correlation between high turbidities and increased sauger catches was made by Doan (1941). Chandler (1942b) pointed out that except for decreased light penetration there was no adverse effect on algae due to suspended inorganic material in the water. An increase in algal production was noted by Verduin (1954) in waters of intermediate turbidity.

It has been demonstrated experimentally that particulate organic material has a beneficial effect on the molting and growth of *Daphnia magna* (Gellis and Clarke, 1935), however the role played by suspended material in natural waters appears to be imperfectly known and the evidence concerning its effect on life in these waters is conflicting. Little experimental work has been done on the relationship of turbidity and turbidity levels to animal and plant life and almost nothing is known concerning the direct interactions of living plankton organisms and the suspended matter.

The material which composes the turbid suspension in natural waters arises primarily from the erosion of the surrounding drainage areas. The weathering products of the soils are, therefore, a significant part of the suspended material. Since the parent rock, climate, topography, and other conditions vary from area to area, the weathering products, such as clay minerals, reflect these variations. These substances have different compositions and characteristics depending upon the place and method of their formation (Grim, 1953).

Clay minerals make up a significant portion of weathered soils. These clay materials are silica, aluminum hydroxides which differ from one another in their crystal lattice structure. Other ions may be substituted for aluminum and silica imparting a charge deficiency to the lattice which is compensated by surface adsorption. The phenomenon of adsorption gives many clay minerals high ion exchange capacities. The ability of this important constituent of normal suspended matter in waters to carry on ion exchange may be another of the subtle, but important, differences between aquatic habitats. Carritt and Goodgal (1954) have emphasized the importance of a "solids-phosphate complex" to the high fertility found in estuaries. Phosphate adsorption and the formation of a "solids-phosphate complex" appears to be favored by acid conditions. Sediments carried by acid river waters are rich in adsorbed phosphate. Contact with the more alkaline waters of the sea causes a release of the phosphate and an enrichment of the estuarine environment. A similar reaction may occur in the vertical circulation in fresh waters in which decomposition in the sediments brings about an acid condition which is favorable to the adsorption of phosphate. During spring and fall turnover the adsorbed phosphate is liberated in the more alkaline surface water (Hayes and Coffin, 1951).

The experiments reported here were designed to determine the effect of different suspended materials on a zooplankter, whose filter feeding habits suggested possible sensitivity to different properties of various suspensions. *Daphnia magna* was chosen because it was easily available, has been extensively studied (Wesenberg-Lund, 1926, MacArthur and Baillie, 1929, Banta, 1939, and Anderson and Jenkins, 1942), and has normally a wide distribution (Pennak, 1953). The effects of glass and charcoal were studied as representing the extremes in adsorptive capacity. It had been previously reported by Marshall and Orr (1952) that the addition of India ink to the medium in which *Calanus finmarchicus*, a filter feeder, was raised had no stimulatory effect on reproduction. For this reason India ink was included in the present investigation.

It was apparent early in the study that the reproductive rate varied considerably from one material to another. An index of reproductive rate was used to report the results of these experiments. The index of reproductive rate used was a ratio of the total number of animals (adults, young, embryos, and eggs) produced from five adult female *D. magna* during an experiment to the duration of the experiment in days and is designated animals per day (A/D). This value was not corrected for the five original animals.

An attempt has been made to compare the conditions of turbidity in the experiments with the conditions found in a turbid planktonic environment. During the spring season, when fluctuations in turbidity were great, measurements were made on the dominant zooplankter, *Daphnia pulex*, the phytoplankter, *Eudorina sp.*, and the total suspended material in a North Carolina farm pond. The clay minerals, which constitute a significant portion of the turbid matter were identified by x-ray diffraction methods.

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Procedures and Methods

STUDIES IN A TURBID POND

Identification of Clay Minerals

A core was taken with a Livingstone corer (Livingstone, 1955, Vallentyne, 1955) from the bottom of Stuart Farm Pond, Cornwallis Road, five miles from the Duke University campus, Durham, North Carolina. The corer penetrated to a depth of 17 cm.

below the mud surface, which was located 169 cm. below the water surface, before striking coarse sand. Portions of the core at 5 cm. intervals were removed and prepared for x-ray. A sample of the water from the pond was also taken, the suspended material allowed to settle out, and this material collected and prepared for x-ray.

The preparation for x-ray was done in the following manner: Samples of the different materials were removed and placed in glass containers. The depth and appearance were recorded. Care was taken to remove the material for the assay from the center of the core to avoid mixing different layers of the sediment. This material was placed in 200 ml. of demineralized water and agitated on a milk shaker for five minutes. The suspension was then decanted off into large clean test tubes and centrifuged at speeds of 480 to 520 rpm. for two minutes. This centrifugation removed the particles larger than clay size. The supernatant, now containing only clay size particles, was decanted into clean test tubes and three drops of saturated calcium acetate were added. The liquid was recentrifuged at high speed to sediment the clay. After the centrifugation the supernatant was discarded and the clay removed to clean 50 ml. beakers and allowed to dry several days in a 40° C. oven. It was then ground to a fine powder with a mortar and pestle, passed through fine copper screen, and stored in small labeled glass vials. For x-ray exposure the powder was packed into a collodion tube (prepared by coating fine copper wire with liquid collodion) and mounted in the x-ray camera. The samples were x-rayed one-half hour at 175 volts and 12 milliamperes using a Hayes X-ray machine with a copper tube. The films were developed in D19B developer and cleared in FIO hypo. The clay minerals were identified by comparing the patterns obtained with those of known clay minerals. In x-rays in which a d-spacing of 14A appeared indicating the presence of montmorillonite, chlorite, or vermiculite, it was necessary to carry out further treatments and x-rays to distinguish which of the three was present. The glycerol solvation technique was employed to determine the presence of montmorillonite. This was done by taking the previously x-rayed powder packed in the collodion tube and dipping the end of the tube in warm glycerol. If the clay mineral present is montmorillonite the process described expands the lattice structure and changes the d-spacing from 14A to 18A, but does not affect the d-spacing of chlorite or vermiculite. To distinguish between these two clay minerals it is necessary to carry out two further processes. One portion of the sample is heated at 500° C. for one-half hour and x-rayed again. A second method consisted of boiling a portion of the sample in NH_4Cl for five minutes, drying, and x-raying again. Under both of these treatments the d-spacing of chlorite normally remains unchanged, but the d-spacing of vermiculite normally shifts from 14A to 10A. Sixteen of the x-ray pictures taken are included in the unpublished thesis (Robinson, 1956).

Measurements of Turbidity and Plankton

Plankton and suspended matter were determined on samples of surface water from Stuart Farm Pond from March 25, 1956, to May 23, 1956. Sampling was done every other day.

For plankton determinations a ten liter sample was taken from a depth of 6 to 18 inches below the surface of the water 12 feet from the shore (Fig. 1) with a Juday plankton trap. The water was concentrated through number 21 silk bolting cloth to about 200 ml. and formalin added immediately. Only the plankton dominants *Daphnia pulex* and *Eudorina* sp. were counted. *Eudorina* counts were made on 1 ml. aliquots in a Sedgewick-Rafter cell. The counts on *Daphnia pulex* were made by evaporating aliquots to dryness in Petri dishes and counting the animals in the residue under a binocular microscope.

A second 600 ml. sample was taken from the top 0 to 3 inches of water. Total suspended material was determined on this sample. The total suspended material (Fig. 4) was determined by passing a 100 ml. aliquot of the surface water through a HA White Grid 047 mm. Millepore Filter (Millepore Filter Corp., Watertown, Mass.) and drying the residue on suction. The filter was weighed before and after filtration and the total suspended material was determined from the difference in weight.

EXPERIMENTS WITH *DAPHNIA MAGNA*

Experimental Studies of Reproduction

Experiments on the reproduction of *Daphnia magna* were carried out in 8 ounce Flint glass jars. Animals used in these experiments were obtained from a stock culture raised in a porcelain refrigerator liner at room temperature under conditions similar to those described by Ryther (1954). Five adult female daphnids were used in each jar. These were examined under a binocular microscope in a depression slide (Slobodkin, 1954) for the presence of eggs and only those with empty brood pouches were used to initiate experiments. A stock suspension of maximum turbidity was first prepared. Various concentrations of suspended material were obtained by diluting the stock suspension. Materials were pulverized in a mortar and pestle and, in the cases of kaolinite, montmorillonite, and pond sediment, were ground several minutes in a Waring Blendor. The pulverized materials were passed through absorbent paper pads (supplied with Millepore Filters) to remove larger particles. The animals were fed daily with various, but equal, quantities of yeast suspension (Slobodkin, 1954). Experiments with each concentration of suspended material were run in duplicate. The concentrations are reported in parts per million (ppm). The reported concentrations were determined as dry weight at the beginning of the experiment. Two 25 ml. aliquots of the most concentrated suspension used were pipetted into weighed aluminum dishes, transferred to a 100° C. drying oven, dried overnight, and weighed immediately upon removal and cooling. To check the final concentrations at the termination of the experiment, the same procedure was carried out. The experiments were conducted at room temperature and the jars were kept covered with inverted aluminum weighing dishes to prevent evaporation. At the end of the experiment the adults (including the original five animals), young, embryos, and eggs were counted and an index of reproductive rate, animals per day (A/D), was used to report the results.

Kaolinite, from Spruce Pine, N. C., montmorillonite, source unknown, and illite, purified from shale from Fithian, Illinois, were obtained from Ward's Scientific Supply Company. Chlorite, from near Chester, Vermont, was obtained from Dr. Roy Ingram, University of North Carolina Geology Department. The charcoal used was Norite A, decolorizing carbon, from the Pfanstiehl Laboratories, Inc.; the glass was pulverized from a Pyrex beaker; and the India ink used was Higgins American Black India Ink.

Observations on Filtering by Daphnia magna

Animals used in the experiment to determine the ability of *D. magna* to filter the suspended material were prepared as follows: one large group of *D. magna* was removed from the stock culture to clear spring water for one hour and a second large group was placed in a concentrated suspension of kaolinite for one hour. Both groups were removed separately and strained through silk bolting cloth. The animals were washed one minute under running tap water, placed in a 100° C. drying oven, dried overnight, and x-rayed. A sample of the kaolinite used to make the suspension was also x-rayed. The results of this experiment proved the ability of *D. magna* to filter kaolinite.

Results and Discussion

The data on reproduction rate of *Daphnia magna* as a function of concentrations of suspended substances are plotted in Figures 1–8. Two distinct effects of suspended inorganic materials on the filter feeding plankter were noted. First, there was a beneficial effect on survival and reproduction at low concentrations, and second, there was a deleterious or toxic reaction at higher concentrations. These effects were found with concentrations of turbid materials similar to those found in the turbid pond which was studied.

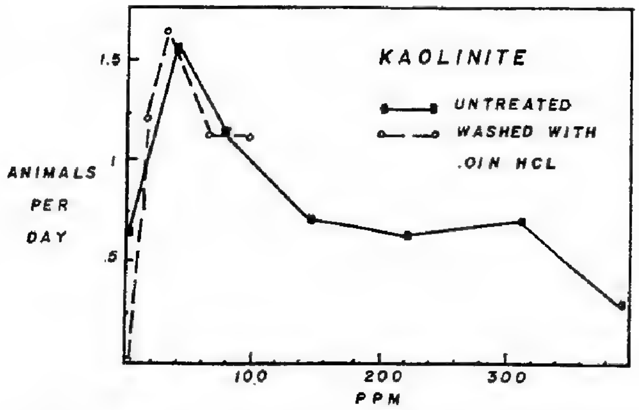

FIG. 1. Reproductive Rate of *Daphnia magna* in Kaolinite. Kaolinite was shown to be non-toxic in levels as high as 392 ppm and to have a peak reproductive rate at 39 ppm. Kaolinite is comparatively unadsorptive and for that reason is apparently not deleterious to *D. magna.* A gradual tapering off of survival and reproduction is noted at higher concentrations. Broken line indicates that washed kaolinite was not more toxic than untreated kaolinite.

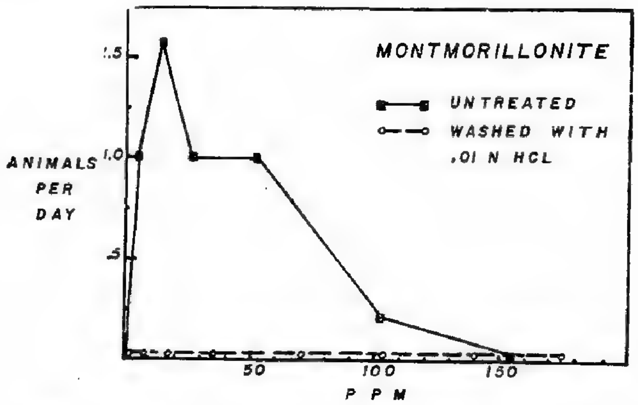

FIG. 2. Reproductive Rate of *Daphnia magna* in Montmorillonite. Montmorillonite was toxic at levels greater than 102 ppm and had a peak reproduction at 13 ppm. This clay mineral is very adsorptive and this property appears to make it toxic to the plankter, *D. magna.* Broken line indicates the increased toxicity in acid washed montmorillonite. No animals survived at any of the levels tested in washed montmorillonite.

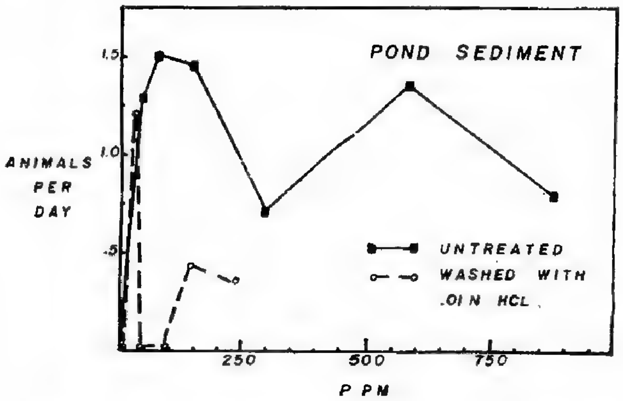

FIG. 3. Reproductive Rate of *Daphnia magna* in Pond Sediment. Pond sediment was not toxic at levels up to 1458 ppm (concentrations as high as 874 shown in Fig. 8) and showed a peak in the reproduction at 73 ppm. Pond sediment was shown to contain kaolinite, vermiculite, illite anl quartz. Dotted line indicates an increase in toxicity due to acid washing.

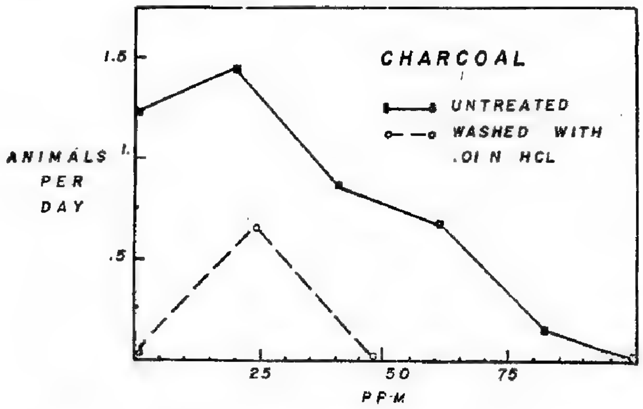

FIG. 4. Reproductive Rate of *Daphnia magna* in Charcoal. Charcoal was toxic at levels greater than 82 ppm and had a peak reproduction at 20 ppm. This material is very adsorptive and apparently this property makes it very toxic to the plankter.

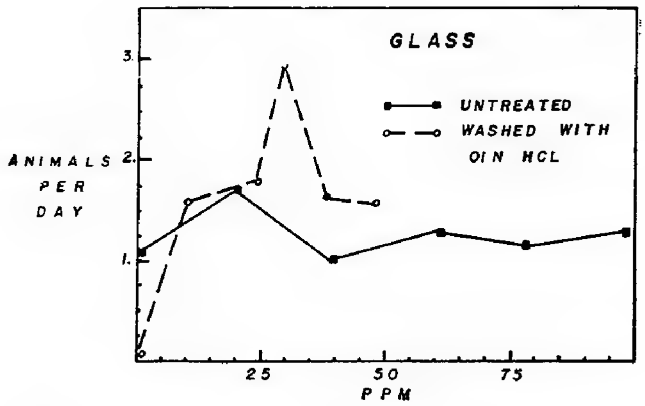

FIG. 5. Reproductive Rate of *Daphnia magna* in Glass. Glass was tested at levels up to 98 ppm and was not found to be toxic at these concentrations. The peak reproduction was recorded at 20 ppm.

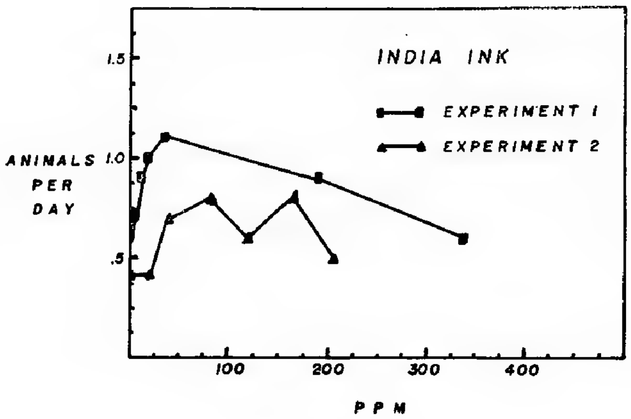

FIG. 6. Reproductive Rate of *Daphnia magna* in India Ink. India ink was tested at levels up to 676 ppm and not found to be toxic. The highest reproduction was recorded at 34 ppm.

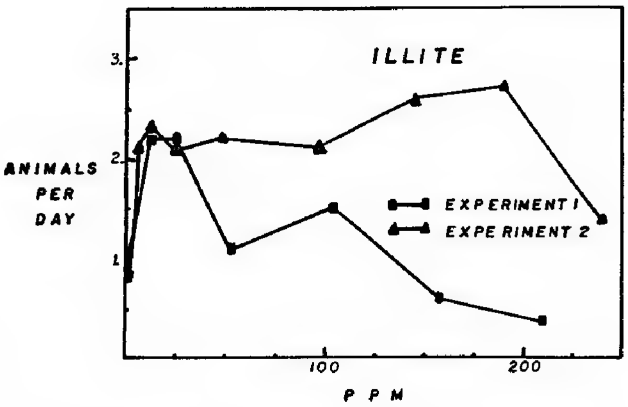

FIG. 7. Reproductive Rate of *Daphnia magna* in Illite. Illite was tested at concentrations as high as 264 ppm and not found to be toxic. The high in reproduction was recorded at 26 and 192 ppm in the first and second experiments respectively.

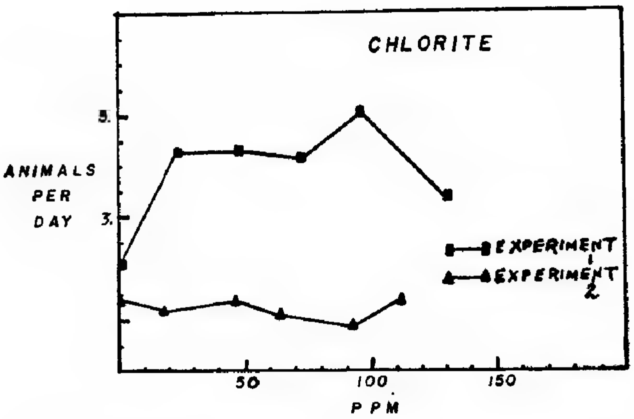

FIG. 8. Reproductive Rate of *Daphnia magna* in Chlorite. Chlorite was tested at levels as high as 120 ppm. In the first experiment the peak reproduction was recorded at 96 ppm. However, in the second experiment the controls were higher than the dilute suspensions, a condition which was not encountered in any other material.

STIMULATORY EFFECT OF LOW CONCENTRATIONS OF SUSPENDED MATTER

It was repeatedly found that *D. magna* did not survive and reproduce optimally without some inorganic suspended matter in the water. Control animals, living in water from which all particles larger than 0.5 u size had been removed by the Millepore Filter, usually died, and, in cases in which death did not occur, the reproductive rate was lower in the controls than in the most dilute suspension. Gellis and Clarke (1935) had previously demonstrated that *D. magna* fails to molt properly without colloidal organic matter in the medium and that particulate matter was beneficial. Their conclusions and the results of the experiments reported here seem to indicate that there is a definite necessity for at least a small amount of suspended material in the medium in which *D. magna* is reared.

A beneficial effect on survival and reproduction at low concentrations of suspended matter was noted in all materials tested. The beneficial effect appeared to depend on the length of the experiments (those run for seven days showed lower reproductive rates than those run for five days) and possibly on other conditions such as temperature. It did not appear to be related in any way to the adsorptive capacity of the suspended material. The A/D ratios (reproductive rates) were 1.57 for kaolinite and montmorillonite (Figs. 1 and 2), 1.5 for pond sediment (Fig. 3), 1.7 for ground glass (Fig. 5), and 1.43 for charcoal (Fig. 4). The A/D ratio for chlorite was 5 (Fig. 8); for illite 2.2 (Fig. 7); and for India ink 1.1 (Fig. 6). The first five materials, montmorillonite, kaolinite, pond sediment, charcoal, and glass were run simultaneously and under the same conditions. The average A/D value for these five substances was 1.55. The reproductive rate for the five materials was similar. The greatest deviation, which was found using ground glass, was only 10 per cent higher than the average value. Illite, chlorite, and India ink gave A/D ratios which varied considerably from the average of the other five materials and from one another despite the fact that these three materials were used under the same conditions and the experiments were conducted simultaneously. Chlorite and illite gave high A/D ratios and India ink gave a low ratio. These three materials were tested for five days at a later time when conditions may have been different. In the instance of India ink there was less reproduction noted than in the presence of any other substance tested. This seems to be in accord with the findings of Marshall and Orr (1952), who showed that India ink did not increase the reproduction of *Calanus finmarchicus*. In their experiments, however, the animals were starved while in these experiments *D. magna* was fed with yeast.

Kaolinite had an A/D ratio of 1.57, while montmorillonite, which is approximately ten times as adsorptive as kaolinite, had the same A/D ratio of 1.57. Thus, the degree of benefit which the suspended material afforded *D. magna* appears to be independent of the adsorptive capacity of the material.

The optimum concentration of turbid matter also appeared to be independent of the adsorptive capacity of the material. The levels at which the highest survival and reproductive rates were recorded ranged from 13 ppm in illite and montmorillonite to 96 ppm in chlorite. The peak reproduction was noted at 39 ppm with kaolinite, 73 ppm in pond sediment, 20 ppm in ground glass and charcoal, and 34 ppm in India ink. Kaolinite and montmorillonite, which have a ten-fold difference in adsorptive ability, have only a three-fold difference in the concentration at which they produce an optimum beneficial effect. It may be that, although the particles in suspension were roughly equal in size in all experiments, having passed through the Millepore Filter absorbent pad, a greater uniformity in experimental conditions may be required before comparisons can be made and conclusions drawn. The need for some suspended material seems apparent and the increased reproduction and survival at concentrations of suspended material less than 100 ppm appear to be evident. These levels are encountered widely in natural environments (Chandler, 1942a, Doan, 1942).

Although there does not appear to be direct correlation between the adsorptive capacity of various materials and the beneficial effect noted at low levels of suspended materials the apparent necessity for some suspended material seems to indicate that an adsorption reaction does occur. All cultures were fed with the same quantities of yeast suspension; therefore, the available food in all instances was essentially identical. The beneficial effect of the suspended matter may arise from some interaction between the suspended particles and the added nutritive substances. This interaction may cause a change in the availability of the nutritive substances. It may adsorb the large organic molecules resulting from decomposition of the yeast cells (Ensminger and Gieseking, 1942, Goring and Bartholomew, 1950) or it may concentrate the final decomposition products such as phosphate and sulphate ions (Carritt and Goodgal, 1954). The concentration of these products may make them more available to the plankter. The surface of the suspended particles with its coating of nutritive materials may also become a fertile site for bacterial activity (Stark *et al.*, 1938, Zobell and Anderson, 1936). It may be that some products of bacterial metabolism are necessary to the plankters. The controls, which did not contain any suspended matter and which presumably had few bacteria (the Millepore Filter removed all particles .5 micron and larger including bacteria), were very unproductive. It may be, then, that the augmentation of reproduction and survival noted with small quantities of suspended matter is due either to a concentration or an alteration of the added nutritive substances. Another possible explanation of the beneficial effect might be the removal of toxic waste products, such as ammonium ions (Anderson, 1944) from the medium to the surface of the suspended particles where they may be rendered either less toxic or less available or might be utilized by bacteria. In all cases it appears likely that adsorption of the material from the medium on to the surfaces of the suspended matter is involved.

Grim (1953) has emphasized the adsorptive quality of the clay minerals. These silica aluminum hydroxides are a significant part of the erosional silt which enters aquatic habitats. Carritt and Goodgal (1954) have demonstrated the uptake of phosphate, sulphate, and other ions by estuarine sediments and the adsorption of carbohydrate phosphates by clays has been shown by Goring and Bartholomew (1950). The role of kaolinite in phosphate fixation has been studied by Murphy (1936) and McAuliffe (1947). There appears to be little doubt that clay minerals can and do operate to concentrate nutritive material on their surfaces. Of what importance this phenomenon is to the economy of the freshwater habitat is poorly understood. It has been shown (Ensminger and Gieseking, 1939, 1941, 1942) that the clay mineral, montmorillonite, forms complexes with proteins and that more protein is adsorbed under acid conditions. Pinck (1954) showed that the adsorbed material occurred as a single layer between the crystal lattice sheets of the clay where it was not available to enzymatic attack. Illite and vermiculite were shown to fix much ammonium ion, while montmorillonite fixed only a small amount (Allison, 1953). There appears then to be an intimate relationship between suspended clay minerals and the nutritive elements which is directly determined by the character of each. Suspended clay minerals must then play a role in growth of all microorganisms in the aquatic environment.

Exactly how and where the nutritive elements adsorbed on suspended matter enter the food cycle of the aquatic habitat is unknown. It has, however, been noted by Whitney (1938) that microstratification, that is, local increases in the turbidity, were associated with increases in the organic material and bacteria. It has long been known (Zobell and Anderson, 1936) that bacterial population growth is roughly proportional to the amount of exposed surface, while Stark *et al.* (1938) have demonstrated an actual concentration of organic matter on submerged surfaces. The evidence for a bacterial intermediate between the food material and the first consumer, the zooplankter, is scanty. Meehan (1937) found no correlation between the amount of dissolved organic matter in the water and the size of the phyto-zooplankton populations. He did, however, suggest that part of the source of the food supply for the zooplankton was closely assciated with the bacteria rather than the phytoplankton. Although it still remains to be clearly demonstrated. there appear to be indications that nutritive materials are adsorbed on to the surfaces of the suspended particles where they are utilized by the bacteria and organized into more complicated molecules which are consumed by the zooplankter. Bacterial production may not be the only result of this adsorptive phenomenon. Verduin (1954) has pointed out that the highest phytoplankton crops in Lake Erie were found in waters of intermediate turbidity. It may be that phytoplankters are also capable of utilizing the adsorbed material because these blooms were associated with increased phosphate introduced by the turbidity.

TOXICITY OF SUSPENDED MATERIAL

At levels greater than those at which the beneficial effect on survival and reproduction was noted a deleterious effect was found with most of the materials tested. This harmful effect appeared to be related to the adsorptive ability of the various materials. Very adsorptive substances such as charcoal (Fig. 4) and montmorillonite (Fig. 2) were toxic at concentrations of approximately 100 ppm. In all other materials (Figs. 1, 3, 6, 7, 8) all of which were less adsorptive than charcoal and montmorillonite, none of the levels tested proved to be toxic, although in all cases except in that of glass (Fig. 4), a distinct tapering off of the reproductive rate was observed. The concentrations of suspended glass were very low (98 ppm highest) because of the difficulty encountered in preparing material which would remain in suspension. It may be that at higher concentrations of ground glass suspension a gradual tapering off of the reproductive rate would be shown. The highest concentrations of other materials tested were kaolinite, 392 ppm (Fig. 1), farm pond sediment, 1458 ppm (Fig. 3 showing values up to 824 ppm), chlorite, 120 ppm (Fig. 8), illite, 264 ppm (Fig. 7), and India ink, 676 ppm (Fig. 6).

THE EFFECT OF ACID WASHED MATERIALS

Five of the materials tested for toxicity level with respect to *D. magna* were treated by washing with dilute hydrochloric acid (Goring and Bartholomew, 1950) and the experiments repeated. This was done to remove all previously adsorbed substances from the suspended material. Kaolinite, montmorillonite, pond sediment, charcoal, and glass were repeated. It was found that washing with acid increased the toxic effect of montmorillonite (Fig. 2), charcoal (Fig. 4) and pond sediment (Fig. 3). Acid washing did not effect the toxicity of glass (Fig. 5) or kaolinite (Fig. 1).

It appears that the toxic effect of the suspended material is related to the adsorptive capacity of that material. The two most adsorptive substances studied, charcoal and montmorillonite, became much more deleterious to *D. magna* after the acid washings. Presumably the washings elute previously adsorbed ions and cause the materials to be more adsorptive and hence more deleterious. No animals were able to survive levels greater than 24 ppm in the treated charcoal (Fig. 4), and all animals at all concentrations died in the treated montmorillonite (Fig. 2). Pond sediment, which was not toxic at any of the levels tested with untreated material, appeared to be much more toxic when treated with the acid (Fig. 3). This may be due to the presence of vermiculite which has adsorptive properties similar to those of montmorillonite (Grim, 1953). Kaolinite (Fig. 1) and glass (Fig. 5), both relatively unadsorptive substances, seemed to have proved that the suspensions used in the untreated state were not toxic due to the presence of adsorbed toxic ions, but rather that their toxicity was a function of their physical ability to adsorb.

In what manner materials with high adsorptive capacities act upon the plankter to bring about this toxic response is not clear. It may be that they adhere to and clog the filter feeding mechanism of the animal or it may be that the weight of the adsorbed material on the carapace causes an increased burden which exhausts and eventually kills it. Many instances were noted in which the animals had difficulty molting and appeared to become entangled in the old carapaces.

OBSERVATIONS IN A TURBID POND

The clay minerals kaolinite, vermiculite (?), and illite were identified from the water and sediment of Stuart farm pond. Quartz was also common in these samples.

The environmental study showed that the materials kaolinite, illite, and quartz, which were not toxic to *D. magna* in the laboratory were not toxic to *D. pulex* in nature. In the southeastern part of this country these materials are commonly found in the soils and, therefore, make up a significant part of the erosional deposition in lakes and ponds. Kaolinite seems to be found most often in areas of acid soil and good drainage. Montmorillonite, which was extremely toxic to *D. magna,* seems to be most characteristic of areas of basic soil and poor drainage (Grim, 1953). The difference in weathering products in various areas is a factor which would appear to be intimately connected with the productivity and animal distribution in these areas. Little work has been done on these relationships. The investigations reported here point up a few for the important differences among clay minerals and how they may affect an aquatic habitat.

Measurements on the plankters found in Stuart farm pond revealed that this relatively turbid environment was apparently quite fertile. At the time of the study, March 25, 1956, to May 23, 1956, there was a bloom of *Eudorina* in the pond. This phytoplankton population reached a peak early in April of nearly 400,000 *Eudorina* per liter (net plankton). At the same time the zooplankton dominant, *Daphnia pulex,* was very common. Late in March *D. pulex* reached a peak of 70 animals per liter. Measurements of the total suspended matter showed that the suspended material in the water decreased steadily from 201 to 30 ppm over the two month period. Heavy rain and wind did not appreciably affect the amount of material in suspension. It was clear that the phytoplankton accounted for a large part of the turbidity. The decline of the phytoplankton probably accounted for much of the decrease in the total suspended matter, although the inorganic content apparently decreased appreciably as well.

Summary

1. The reproductive rate of *Daphnia magna* was studied in cultures containing 0–1458 ppm of suspended materials. These materials were shown to be filtered and passed through the gut of the daphnid.

2. Small amounts of suspended material seem to be essential to the optimal survival and reproduction of *D. magna* so that in dilute suspensions a beneficial effect was noted with all materials tested. This effect appeared to be unrelated to the adsorptive capacities of the suspensions, whereas at higher levels some suspensions had a toxic effect which was apparently related to their adsorptive capacities.

3. Charcoal (tested at levels up to 102 ppm) and montmorillonite (154 ppm), the most adsorptive materials studied, were toxic at approximately 100 ppm; ground glass (98 ppm), India ink (676 ppm), kaolinite (392 ppm), chlorite (120 ppm), illite (264

ppm), and pond sediment, in which kaolinite, vermiculite (?), illite, and quartz were identified by x-ray diffraction (1458 ppm), were not toxic at any of the tested levels.

4. Washing in .OIN HCl increased the toxicity of adsorptive materials, montmorillonite, charcoal, and pond sediment, but did not increase the toxicity of glass or kaolinite.

5. The turbidity of a typical North Carolina farm pond was found to vary over the range of concentrations 30–201 ppm which were shown to be beneficial and toxic in turbidity experiments. The plankton dominants *Eudorina* sp. and *Daphnia pulex* were measured over the same spring period during which the turbidity fluctuation was studied.

LITERATURE CITED

Allison, F. E., M. Kefauver, and E. M. Roller. 1953. Ammonium Fixation in Soils. Soil Sci. Soc. Am. Proc., 17: 107–110.

————, E. M. Roller, and J. E. Doetsch. 1953. Ammonium Fixation and Availability in Vermiculite. Soil Sci., 75: 173–180.

Anderson, B. G. 1944. The Toxicity Thresholds of Various Substances Found in Industrial Wastes as Determined by the Use of *Daphnia magna.* Sewage Works Jour., 16: 1156–1165.

———— and J. C. Jenkins. 1942. A Time Study of the Life Span of *Daphnia magna.* Biol. Bull., 83: 260–272.

Banta, A. M. 1939. Studies on the Physiology, Genetics, and Evolution of Some Cladocera. Carnegie Inst. of Wash. Dept. of Genetics., 40: 1–285.

Carritt, D. E., and S. Goodgal. 1954. Sorption Reactions and Some Ecological Implications. Deep Sea Research, 1: 224–243.

Chandler, D. C. 1942a. Limnological Studies of Western Lake Erie. II. Light Penetation and Its Relation to Turbidity. Ecology, 23: 41–52.

————. 1942b. Limnological Studies of Western Lake Erie. III. Phytoplankton and Physical Chemical Data from November 1939–November 1940. Ohio Jour. Sci., 42: 24–44.

Doan, K. H. 1941. Relation of Sauger Catch to Turbidity on Western Lake Erie. Ohio Jour. Sci., 41: 449–452.

————. 1942. Some Meteorological and Limnological Conditions as Factors in the Abundance of Certain Fishes in Lake Erie. Ecol. Monog., 12: 293–314.

Ellis, M. M. 1936. Erosional Silt as a Factor in Aquatic Environments. Ecology, 17: 29–42.

Ensminger, L. E., and J. E. Gieseking. 1939. The Absorption of Proteins by Montmorillonitic Clays. Soil Sci., 48: 467–473.

————. 1941. The Absorption of Proteins by Montmorillonitic Clays and Its Effect on Base Exchange Capacity. Soil Sci., 51: 125–132.

————. 1942. Resistance of Clay Adsorbed Proteins to Proteolytic Hydrolysis. Soil Sci., 53: 205–209.

Frank, P. 1952. A Laboratory Study of Intraspecific and Interspecific Competition in *Daphnia pulicaria* (Forbes) and *Simocephalus vetulus* O. F. Muller. Phys. Zool., 25: 178–204.

Gellis, S. S., and G. L. Clarke. 1935. Organic Matter in Dissolved and Collodial Form as Food for *Daphnia magna.* Phys. Zool., 8: 127–137.

Goring, C. A. I., and W. V. Bartholomew. 1950. Adsorption of Carbohydrate Phosphates by Clays. Proc. Soil Sci. Soc. Amer., 15: 189–194.

Grim, R. E. 1953. Clay Mineralogy. New York, McGraw-Hill, pp. 1–327.

Hayes, F. R., and C. C. Coffin. 1951. Radioactive Phosphorus and Exchange of Lake Nutrients. Endeavour, 10: 78–81.

Livingstone, D. A. 1955. A Lightweight Piston Sampler for Lake Deposits. Ecology, 36: 137–139.

MacArthur, J. W., and W. H. T. Baillie. 1929. Metabolic Activity and Duration of Life. I. Influence of Temperature on Longevity of *Daphnia magna.* J. Exp. Zool., 53: 221–242.

Marshall, S. M., and A. P. Orr. 1952. On the Biology of *Calanus finmarchicus.* VII. Factors Affecting Egg Production. J. Mar. Biol. Assn. U. K., 30: 527–548.

————. 1955. The Biology of a Marine Copepod. London, Oliver and Boyd, pp. 1–188.

McAuliffe, C. D., N. S. Hall, L. A. Dean, and S. B. Hendricks. 1947. Exchange Reactions Between Phosphate and Soils: Hydroxylic Surfaces of Soil Minerals. Proc. Soil Sci. Soc. Amer., 12: 119–123.

Meehan, O. L. 1937. The Relative Importance of Plankton Constituents in Bass Ponds as Measured by Organic Content. Int. Rev. ges. Hydrobiol. u. Hydrogr., 36: 131–137.

Meyer, B. S., and A. C. Heritage. 1941. Effect of Turbidity and Depth of Immersion on Apparent Photosynthesis in *Ceratophyllum demersum.* Ecology, 22: 17–22.

Moore, E. 1937. The Effect of Silting on Productivity of Waters. Trans. N. Amer. Wildl. Conf., 2: 658–661.

Murphy, H. F. 1939. The Role of Kaolinite in Phosphate Fixation. Hilgardia, 12: 343–382.

Pennak, R. W. 1953. Fresh Water Invertebrates of the United States. New York, The Ronald Press, pp. 1–769.

Pinck, L. A., R. S. Dyal, and F. E. Allison. 1954. Protein Montmorillonitic Complexes, Their Properties and the Effect of Soil Microorganisms on Their Decomposition. Soil Sci., 78: 109–118.

Ruttner, F. Translated by D. G. Frey and F. E. Fry. 1953. Fundamentals of Limnology. Toronto, University of Toronto Press, pp. 1–242.

Ryther, J. H. 1954. Inhibitory Effects of Phytoplankton Upon the Feeding of *Daphnia magna* with Reference to Growth, Reproduction, and Survival. Ecology, 35: 522–533.

Slobodkin, L. B. 1954. Population Dynamics in *Daphnia obtusa* Kurz. Ecol. Monogr., 24: 69–88.

Stark, W. H., J. Stadler, and E. McCoy. 1938. Some Factors Affecting the Bacterial Population of Freshwater Lakes. J. Bacteriol., 36: 653.

Vallentyne, J. R. 1955. A Modification of the Livingstone Piston Sampler for Lake Deposits. Ecology, 36: 139–141.

Verduin, J. 1954. Phytoplankton and Turbidity in Western Lake Erie. Ecology, 35: 550–561.

Wallen, I. E. 1951. The Direct Effect of Turbidity on Fishes. Bull. Okla. Agri. and Mech. Coll., Biol. Ser. 2, 48: 1–27.

Welch, P. S. 1952. Limnology. New York, McGraw-Hill, pp. 1–538.

Wesenberg-Lund, C. 1926. Contributions to the Biology and Morphology of the Genus Daphnia. Memoires de l'Academie Royale des Sciences et des Lettres de Danemark, Copenhague, Section des Sciences, 8^{me} serie, 11 (2) : 91–250.

Whitney, L. 1938. Microstratification of Inland Lakes. Trans. Wisc. Acad. Sci. Arts Lett., 31: 155–173.

Zobell, C., and D. Anderson. 1936. Observations on the Multiplication of Bacteria in Different Volumes of Stored Sea Water and the Influence of Oxygen Tension and Solid Surfaces. Biol. Bull., 71: 324–342.

The Acanthocephalan Parasites of the Fishes of the Texas Coast

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In the course of a histochemical study of the Acanthocephala during the 1955–56 school year at Rice Institute in Houston, 1,264 fish from the coastal waters of Texas, representing 39 species, were examined for Acanthocephala. These fish, for the most part, were seined on the open Gulf beach or in the tidal creeks and pools. A few fish were taken by hook and line and one batch was received from local fishermen in Galveston Bay. Generally, the fish were collected on Saturday and kept in crushed ice until the following Monday. It was found that all the parasites except a few of the more delicate trematodes were still alive, and, on the basis of the histochemical tests, the Acanthocephala appeared to be in good physiological condition. Since it was desirable for the histochemical studies that the worms be fixed as soon after removal from the fish as possible, the examinations were done on a composite basis. Thus no individual host-parasite records were obtained but an accurate count was made of the number of worms recovered from each composite. Such records at least give an indication of the density of the parasite population although for detailed study it would be desirable to keep more exhaustive records. Inasmuch as 7 species representing 4 families and including one new genus and species were found during the course of these collections it was thought advisable that these collection records be published. Table 1 shows the fish species examined and the collection data.

All the Acanthocephala used in this survey were relaxed in distilled water to bring about the extrusion of the proboscis, fixed in Bouin's fixative and stained in picrocarmine. All specimens are in the collection of W. L. Bullock, Zoology Department, University of New Hampshire, Durham, New Hampshire.

FAMILY RHADINORHYNCHIDAE

Telosentis tenuicornis (Linton, 1892) Van Cleave, 1947

This parasite has been reported from a wide variety of marine fish of the Atlantic coast from Woods Hole to the Gulf of Mexico. In the latter area it has previously been reported by Chandler (1935) from *Micropogon undulatus*, *Leiostomus xanthurus*, and *Polydactylus octonemus*. During the present study this form has also been obtained from *Cynoscion arenarius* and *Orthopristis chrysopterus*. *T. tenuicornis* was collected as follows:

From *Micropogon undulatus*		
1 worm from 1 fish	East Galveston Beach	10–15–55
92 worms from 23 fish	Redfish Bank, Galveston Bay	10–16–55
From *Leiostomus xanthurus*		
4 worms from 1 fish	East Galveston Beach	10–15–55
1 worm from 1 fish	East Galveston Beach	4–28–56

From *Cynoscion arenarius*
1 worm from 1 fish Redfish Bank, Galveston Bay 10–16–55
From *Orthopristis chrysopterus*
2 worms from 1 fish Galveston ferry slip 11–19–55

One immature female obtained from *Fundulus grandis* at Riviera Beach appears to belong to this species and was so indicated by Bullock (1957, in press). However, although all other measurements conform to those given for *T. tenuicornis* by Chandler (1934), this specimen has 28 hooks per row instead of the 22–24 previously recorded for this species. The small genital papillae characteristic of the genus were clearly seen.

Illiosentis furcatus Van Cleave and Lincicome, 1939

The original description of *Illiosentis furcatus* was based on a series of worms from the southern kingfish, *Menticirrhus americanus.* At the same time the genus *Illiosentis* was proposed to include this species on the basis of a series of highly distinctive char-

Table 1
Fishes Examined During this Survey

Host	Number Examined	Number of Collections	Number of Collections with Acanthocephala
Elops saurus	1	1	0
Brevoortia gunteri	13	2	0
Anchoviella mitchilli	26	6	0
Bagre marina	4	3	0
Galeichthys felis	33	9	4
Lucania parva	4	2	0
Fundulus grandis	104	17	3
Fundulus similis	157	13	0
Fundulus pulvereus	10	3	0
Adinia multifasciata	34	3	0
Cyprinodon variegatus	428	19	16
Mollienisia latipinna	22	5	0
Syngnathus sp.	1	1	0
Menidia beryllina	76	8	0
Mugil cephalus	68	16	1
Polydactylus octonemus	77	7	2
Trichiurus lepturus	2	2	0
Caranx hippos	4	1	0
Trachinotus carolinus	11	2	0
Oligoplites saurus	3	1	0
Orthopterus chrysopterus	1	1	1
Lagodon rhomboides	10	3	0
Archosaugus probatocephalus	2	1	0
Eucinostomus sp.	1	1	0
Bairdiella chrysura	3	2	0
Stellifer lanceolatus	6	1	0
Sciaenops ocellatus	29	4	0
Leiostomus xanthurus	12	6	2
Micropogon undulatus	51	5	2
Menticirrhus americanus	21	4	1
Menticirrhus littoralis	6	2	2
Cynoscion arenarius	12	3	1
Cynoscion nebulosus	1	1	0
Chaetodipterus faber	2	2	0
Gobionellus boleosoma	11	2	0
Gobisoma bosci	8	2	0
Astrocopus y-graecum	7	2	0
Paralichthys lethostigmus	1	1	0
Labrisomus nuchipinnis	2	1	0

acteristics. This original material came from Grand Isle, Louisiana. Since that time the only published report of the occurrence of this acanthocephalan is that of Chandler (1954) who refers to the presence of this species in *M. americanus* in Corpus Christi Bay. During the present study this parasite was found as follows:

From *Menticirrhus americanus*		
3 worms from 3 fish	Isla Blanc Park, Port Isabel	4–21–56
From *Menticirrhus littoralis*		
2 worms from 4 fish	10 miles west of Sabine Pass	1–14–56
1 worm from 2 fish	Surfside Beach	3– 3–56
From *Polydactylus octonemus*		
3 worms from 31 fish	Gilchrist	4– 7–56

While the worms that were collected and studied as whole mounts conformed to the original published description of *I. furcatus* in nearly all points, there were a few differences that ought to be noted. The 3 worms from the threadfin, *Polydactylus octonemus* were immature and, since this genus of acanthocephalans appears to be restricted to members of the genus *Menticirrhus* and closely related genera (Van Cleave, 1945), it is probable that these parasites of the threadfin were in an abnormal host and the record constitutes an accidental infection. It is of interest, however, that the lemnisci of all 3 of these worms were very distinctly forked near the tips. Such a condition was not present in specimens from *M. americanus* collected in this study nor in type material borrowed from the U. S. National Museum. Van Cleave and Lincicome characterized the lemnisci as "long, cylindrical." Unfortunately for this study, the worms from *M. littoralis* had already been used for enzyme studies following a spot identification on the basis of host genus, the structure of the proboscis, and the nature of the posterior end of the female.

The specimens from the type host *(M. americanus)* presented even more difficulties. In this material the proboscis hooks had a shape considerably different from that of the other material and the original description. In the type material and the specimens from *P. octonemus* the hooks of the dorsal surface of the proboscis are regionally modified so that the hooks of the anterior and middle region are slender thorn-shaped hooks whereas the basal hooks are stubby and sharply recurved. This transition to the recurved hooks is abrupt and takes place at about the level of the eleventh or twelfth hook from the base of the probosics. This condition is clearly shown in Figure 2 of Van Cleave and Lincicome's paper. The hooks of the ventral surface of the proboscis are unmodified and show only the gradual decrease in size. In the specimens from the type host collected at Surfside Beach the hooks remain long and slender but the tips of these hooks are recurved after the fashion of a linoleum knife. This peculiar modification of the hooks takes place on both the dorsal and ventral surfaces (and apparently laterally as well). Furthermore, it occurs gradually and there is no abrupt transition from the simple hooks to those with recurved tips. Such a unique hook shape could conceivably warrant the erection of a new species. However, these 3 specimens are here considered a variety of the species on the basis of their occurrence in the type host species and their comformity to the description of *I. furcatus* in nearly all other points. Certainly a study of a long series of specimens from the Gulf coast would be highly desirable. It is of interest that specimens of *I. furcatus* taken from the northern kingfish, *M. saxatilis,* by the author at Woods Hole, Massachusetts (unpublished observations) conform to the original material in all points except a slightly larger hook size.

FAMILY GORGORHYNCHIDAE

Gorgorhynchus gibber Chandler, 1934

This acanthocephalan was described by Chandler (1934) from worms obtained from "2 out of 3 specimens of the marine catfish, *Galeichthys felis,* taken near Bolivar Point in the Gulf of Mexico." During the present study 33 specimens of *G. felis* and 4 specimens of the related *Bagre marina* were examined but no specimens of *Gorgorhynchus gibber* were found. Of the fish examined 14 were collected at the entrance to Galveston Bay, near Bolivar Point, between September 19, 1955 and April 30, 1956.

Serrasentis socialis (Leidy, 1851) Van Cleave, 1924

S. socialis was first descibed by Leidy (1851) from the intestines of "*Platessa plana.*" Van Cleave (1924), in his critical study of the Leidy material, clearly differentiated this form from *E. gadi* with which Leidy had confused it in his "*E. socialis,*" and erected the genus *Serrasentis.* He further indicated that this genus should be associated with *Rhadinorhynchus.* Larval forms have been described from the mesenteries of numerous marine fishes of the Atlantic coast. The greatest number of such collections are those of Linton who referred to this worm as *Echinorhynchus sagittifer.* The only recorded collections of adults are those of Linton from *Rachycentron canadus* at Beaufort, North Carolina, and Ward (1954) from *Trachinotus falcatus* at Miami, Florida. Hitherto there have been no records of this worm in the Gulf of Mexico. During the present study numerous worms were taken from the mesenteries of *Galeichthys felis* at Galveston and Port Isabel. Since most of these worms were undergoing destruction by the host tissues and were mixed in with cestode larvae undergoing similar destruction, no counts could be made of the numbers present, and only 3 living specimens were recovered. It is probable that the definitive host is a species of fish more common in the deeper waters of the Gulf or one that comes inshore during the warmer summer months, not included in this study.

Nipporhynchus ornatus (Van Cleave, 1918)

Filisoma fidum Van Cleave and Manter, 1947

Neither of these acanthocephalans were collected during the present study. This is most likely due to collecting being restricted to the close inshore region of the coast. *N. ornatus* has been reported from several species of marine fishes but appears to occur most commonly in the grunts *(Hæmulidae)* and the snappers *(Lutianidae).* Since these fish are offshore reef fishes they are poorly represented in this study. It is probable that *N. ornatus* occurs in these fish but it is so far unreported from the Texas coast. *F. fidum* has been reported only from the Bermuda chub *(Kyphosis sectatrix).* Since this fish is apparently more tropical in its distribution than the hosts of *N. ornatus* it may not occur in the northern Gulf.

FAMILY POLYMORPHIDAE

Arhythmorhynchus duocinctus Chandler, 1935

This acanthocephalan is found encysted in the mesenteries of fish and develops to maturity in birds. It was first described by Chandler (1935) from the mesenteries of *Paralichthys lethostigmus* in Galveston Bay. The mature worms were found and described by Lincicome (1943) from the black-crowned night heron in New York. While this worm is probably widespread in its distribution, Chandler found only 8 specimens of *A. duocinctus* in one of two *P. lethostigmus.* Only 2 specimens were recovered from the mesenteries of one of 7 *Fundulus grandis* seined in East Bay at Gilchrist on January 21, 1956.

FAMILY NEOECHINORHYNCHIDAE

Octospiniferoides chandleri Bullock, 1957

This species of neoechinorhynchid acanthocephalan was described on the basis of 2 immature female worms taken from the intestine of 3 *Fundulus grandis.* These fish were seined in East Bay at Gilchrist on April 7, 1956. No other specimens of this parasite were obtained from 100 other *F. grandis* collected at this and other localities along the Texas coast. Over 600 additional cyprinodontid fishes representing 5 species (see Table 1) were likewise negative for this parasite. Since these infected fish were collected immediately prior to the period of least abundance of the species (Gunter, 1945) it was difficult to obtain more host specimens and none of those obtained were infected. It is possible that this parasite may be more common during the summer peak of abundance of the host species. Further evidence for this is found in the immaturity of the only specimens of *O. chandleri* found. Unfortunately, the further study of this problem had to be discontinued because of our return to New Hampshire.

Atactorhynchus verecundus Chandler, 1935

A. verecundus was first reported and described by Chandler (1935) from Galveston Bay. Since that time no record of its occurrence has appeared in the literature. Sparks (1956) in an extensive (though as yet unpublished) study of the trematodes of Gulf of Mexico fishes informs me that several years ago he sent some acanthocephalans from *Cyprinodon variegatus* to Dr. Van Cleave for identification. Inasmuch as I have obtained this parasite from the fish of the same pool at Port Aransas it is probable that Sparks collected *A. verecundus.* This acanthocephalan is most noteworthy because of its rigid host specificity. Nearly every population of this host on the Texas coast appears to support this worm but examination of several hundred fish of a wide variety of species, including other cyprinodontids, has failed to turn up even a single immature specimen from anything but this one host. From the data included below it can be seen that the parasite is apparently more common in the southern part of its range. The degree of infection in the small tidepool at the Institute of Marine Science would make this a good place to investigate the life history of this acanthocephalan.

A. verecundus was collected as follows:

3	worms	from	20	fish	East Bay; Gilchrist	11–19–55
7	"	"	21	"	Clear Lake, Galveston Bay	12– 3–55
1	"	"	7	"	Seabrook, Galveston Bay	12– 3–55
36	"	"	35	"	Aransas Bay, Fulton	12–21–55
1	"	"	3	"	Aransas Bay, Rockport	12–22–55
2	"	"	53	"	Trinity Bay; near Baytown	1– 7–56
33	"	"	36	"	East Bay; Gilchrist	1–21–56
26	"	"	106	"	West Bay; near Surfside Beach	3– 3–56
1	"	"	7	"	Laporte, Galveston Bay	3–10–56
10	"	"	1	"	Clear Lake, Galveston Bay	3–17–56
35	"	"	30	"	East Bay; Gilchrist	4– 7–56
15	"	"	29	"	East Bay; Gilchrist	4–25–56
15	"	"	10	"	Seabrook, Galveston Bay	5– 2–56
40	"	"	17	"	Aransas Bay; Fulton	5– 5–56
150	"	"	20	"	Port Aransas	5– 5–56
2	"	"	17	"	San Luis Pass, West Galveston	5–16–56

Floridosentis elongatus Ward, 1953

F. elongatus has been reported from the striped mullet, *Mugil cephalus*, from Florida by Ward (1953, 1954) and from Puerto Rico by Cable and Quick (1954). In the present study 1 male specimen was obtained from one of 13 mullet seined at "Neritina flat" (Hedgpeth, 1953) in the Laguna Madre near Port Isabel. It is of interest that this parasite was not found in any of the 55 mullet seined between Gilchrist and Port Aransas. On the basis of the reported distribution of this parasite, its absence from the upper Texas coast may indicate that its life cycle involves an intermediate host that is limited to warmer waters.

LITERATURE CITED

Bullock, W. L. 1957. *Octospiniferoides chandleri* n. gen., n. sp., a neoechinorhynchid acanthocephalan from *Fundulus grandis* Baird and Girard on the Texas coast. J. Parasit., 43: 97–100.

Cable, R. M., and L. A. Quick. 1954. Some Acanthocephala from Puerto Rico with the description of a new genus and three new species. Trans. Amer. Micros. Soc., 73: 393–400.

Chandler, A. C. 1934. A revision of the genus *Rhadinorhynchus* (Acanthocephala) with descriptions of new genera and species. Parasit., 26: 351–358.

————. 1935. Parasites of fishes in Galveston Bay. Proc. U.S. Natl. Mus., 83: 123–157.

————. 1954. Acanthocephala. In "Gulf of Mexico. Its Origin, Waters and Marine Life." Fish. Bull., U.S., 55: 355.

Gunter, G. 1945. Studies on marine fishes of Texas. Publ. Inst. Mar. Sci., Univ. Texas, 1: 1–190.

Hedgpeth, J. W. 1953. An introduction to zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. Publ. Inst. Mar. Sci. Univ. Texas, 3: 107–224.

Leidy, J. 1851. Descriptions of new species of Entozoa. Proc. Acad. Nat. Sci., Phila., 5: 155–156.

Lincicome, D. 1943. Observations of the adult *Arhythmorhynchus duocinctus Chandler*, 1935 (Polymorphidae, Acanthocephala.) Trans. Amer. Micros. Soc., 62: 69–71.

Sparks, A. 1956. Personal communication.

Van Cleave, H. J. 1924. A critical study of the Acanthocephala described and identified by Joseph Leidy. Proc. Acad. Nat. Sci., Phila., 76: 279–334.

————. 1945. A new species of the acanthocephalan genus *Illiosentis* (Rhadinorhynchidae). J. Parasit., 31: 57–60.

Van Cleave, H. J., and D. R. Lincicome. 1939. On a new genus and species of Rhadinorhynchidae (Acanthocephala). Parasit., 31: 413–416.

Ward, H. 1953. A new genus and species, *Floridosentis elongatus*, of Neoechinorhynchidae (Acanthocephala). J. Parasit., 39: 392–394.

————. 1954. Parasites of marine fishes of the Miami region. Bull. Mar. Sci. Gulf and Carib., 4: 244–261.

Body Fluid of the Oyster *Crassostrea virginica*[1]

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A voluminous literature is available concerning the biology of the oysters *Ostrea* and *Crassostrea*. However, little information concerning regulation of their body fluid has been published. Nelson (1938) postulated that the genus *Crassostrea* armed with a superior cleansing mechanism, the promyal chamber, has in its evolution been able to invade the upstream zones of its environment in contrast to *Ostrea* that remained in the sea or at least in waters of higher salinity. Specimens of *Crassostrea* should, therefore, be better osmoregulators than specimens of *Ostrea*. In addition, Stauber (1950) demonstrated that three distinct physiological varieties of *Crassostrea virginica* occur along the Atlantic Coast with critical spawning temperatures of 16.4° C. in Long Island Sound, 20° C. in the Bideford River, Prince Edward Island, Canada, and 25° C. in Delaware Bay.

Blood and pericardial fluid of a Japanese oyster, *Ostrea circumpicta*, remained hypertonic to the environment but the salinity of these fluids followed changes in environmental salt concentration. Pericardial fluid had a lower chloride concentration than blood (Yazaki, 1929). Dr. Imai of Japan has informed Dr. Thurlow C. Nelson that he is practically certain the oyster referred to as *Ostrea circumpicta* by Yazaki was actually *Crassostrea nippona*. The authors are indebted to Dr. Nelson for relaying this information. The reason for believing the name used by Yazaki was incorrect is that *Ostrea circumpicta* is larviparous and belongs to the salt water flat type of oyster whereas *Crassostrea nippona* is oviparous and does not belong to the salt water flat type.

Loosanoff (1952) showed that the salinity of the body fluid of *Crassostrea virginica* followed changes in salinity of the surrounding water. In general, shell fluid was more dilute than the environment. Body fluid had an even lower concentration than shell fluid. Fingerman and Fairbanks (1956) also showed that the body fluid of the oyster *Crassostrea virginica* followed changes of salinity of the environment. However, the blood tended to change less than the other fluids, indicative of a limited ability to osmoregulate.

Louisiana oysters shucked with injury to the mantle during May, June, and July, 1955, lost an average of 53.7 percent of their original body weight in 60 minutes. Weight decrease was due to loss of body fluids when oysters were removed from the shells (Fingerman and Fairbanks, 1956). Gunter (1942) demonstrated that the extent of decrease of body volume of shucked Texas oysters, presumably due to loss of body fluid, depended upon the time of year. Greatest decrease of body volume occurred in October and the least in March.

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[1] This investigation was conducted under a contract between Tulane University and the United States Fish and Wildlife Service. Funds were made available under provisions of P.L. 466, 83rd Congress, approved July 1, 1954, commonly called the Saltonstall-Kennedy Act.

George and Ferguson (1950) described the blood of the gastropods *Busycon carica, Busycon canaliculatum,* and *Fasciolaria tulipa.* Cells comprised from slightly less than one percent to two percent of the blood volume. The blood did not coagulate when the gastropods were bled. Three cell types were present: (1) lymphoid cells, (2) granular macrophages, (3) eosinophilic granular amoebocytes.

The present investigation was undertaken to extend the observations of Fingerman and Fairbanks (1956) on the body fluid of the Louisiana oyster *Crassostrea virginica* and to compare body weight losses of Northern and Southern oysters shucked during the spring and fall. Among other factors considered were numbers of cells and concentrations of chloride and proteinaceous materials in body fluid. The term "proteinaceous material" is used because not all of this material appeared to have a molecular size similar to that of true proteins.

Materials and Methods

Specimens of the oyster *Crassostrea virginica* used in the experiments described below were obtained from three localities, Delaware Bay, Chesapeake Bay, and Louisiana. The vast majority of the Louisiana oysters were from Barataria Bay.

Oysters were maintained in large plexiglass aquaria containing recirculating sea water filtered through glass wool and charcoal. Salinity of the water in the aquaria was usually maintained at 17 p.p.t. Oysters were acclimatized to the water in the aquaria for at least 24 hours before being used in an experiment with but two exceptions that will be mentioned below.

Determination of chloride concentration was performed according to the method of Schales and Schales (1941). To determine concentrations of proteinaceous materials the volume of precipitate obtained by addition of one percent phosphotungstic acid solution to body fluid was compared with the volume of precipitate obtained from addition of the phosphotungstic acid solution to a one percent albumen solution. The volumes of precipitates were compared after centrifugation.

Results and Discussion

BODY WEIGHT OF OYSTERS

Data presented below illustrative of weight changes of oysters were not presented in grams but as percentages of the original body weight. Figure 1 was, therefore, prepared to show the body weight range of Louisiana oysters used during 1956 in experiments where body weight was determined. The figure represents the weights of 393 oysters. Some of the oysters were used in the experiments reported below and others were not. The majority of the oyster bodies, 81.2 percent, weighed from 16 to 35 grams.

Body and shell weights of 608 Louisiana oysters were determined during 1955 and 1956. Body weight was 17.9 percent of the total weight of shells plus body.

BODY FLUID LOSSES OF NORTHERN VERSUS SOUTHERN OYSTERS

This set of experiments was designed to determine and compare the amount of internal body fluid lost by Northern and Southern oysters in the spring and fall after

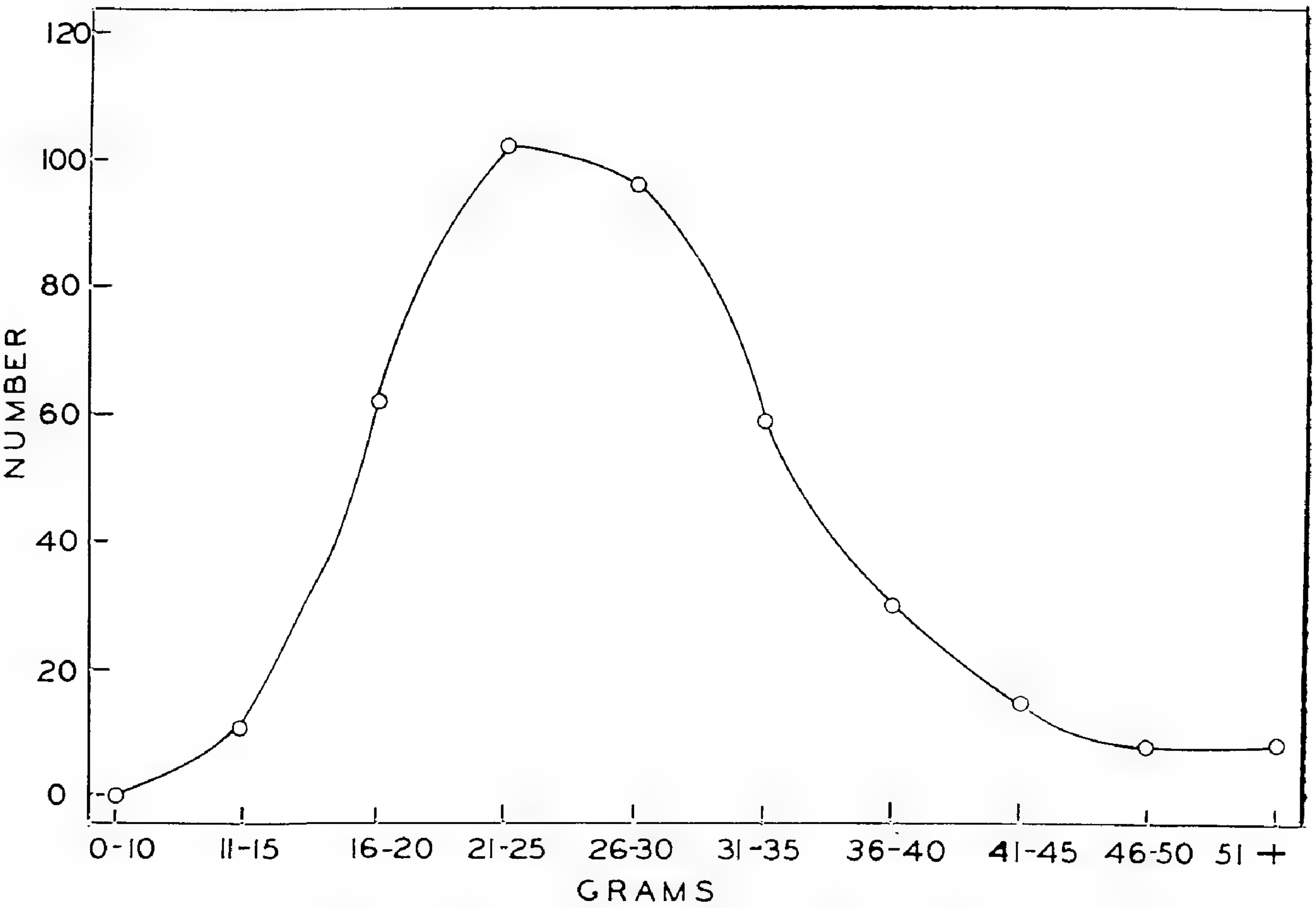

FIG. 1. Body weight distribution of Louisiana oysters.

shucking. Oysters were shucked and weighed in the manner described by Fingerman and Fairbanks (1956). Bodies of 19 oysters were removed from their shells and placed in containers. The initial body weight including the escaping internal body fluids was then determined. During the shucking process the mantle in the region of the adductor muscle was routinely ruptured. The bodies were then weighed, without the fluid that had escaped, 15, 30, and 60 minutes after the oysters had been shucked. Weights were expressed as percentages of the original body weight. Values for the 19 oysters used in each experiment were averaged.

Oysters to be shucked were obtained from three localities. Louisiana oysters, the vast majority grown in Barataria Bay, were obtained from the Martina and Martina Oyster Company, New Orleans. Chesapeake Bay oysters were shipped by the Woodfield Fish and Oyster Company, Galesville, Maryland. Delaware Bay oysters were obtained from the Port Norris Oyster Company, Port Norris, New Jersey. Three days were usually required for arrival of Northern oysters in New Orleans. Oysters were shucked after they had been in sea water aquaria for at least 24 hours with but two exceptions. Oysters that arrived in the laboratory on March 20 and 23 were shucked the same day. These experiments were performed during March, April, October and November of 1956. Results of individual experiments are presented in Table 1. Data of individual experiments were also averaged according to source of the oysters and season of collection (Table 1). As evident from inspection of Table 1, most of the weight loss occurred in the first 15 minutes after shucking.

Oysters from the three localities that were shucked in the spring lost nearly the same amount of body fluid, a difference of merely 3.1 percent was evident among the groups 60 minutes after they had been shucked. But when oysters from the three localities were

Table 1

Relation Between Geographical Source, Season and Body Weight of Shucked Oysters. Weights are expressed as the percentage of the original body weight.

		Minutes After Shucking		
Source	Date Shucked	15	30	60
New Jersey	March 19	55.7	53.1	52.3
(Delaware Bay)	March 30	61.2	57.8	56.4
	Average	58.5	55.5	54.4
	October 9	53.2	51.4	50.5
	October 11	52.3	50.7	49.8
	October 16	70.8	69.9	68.5
	October 18	65.5	63.9	63.0
	October 30	56.3	55.0	53.7
	Average	59.6	58.2	57.1
Maryland	March 20	52.8	50.8	49.7
(Chesapeake Bay)	April 5	56.2	54.5	52.8
	Average	54.5	52.7	51.3
	October 11	44.9	42.8	41.8
	October 16	37.1	34.8	34.0
	October 23	43.7	42.0	40.8
	October 25	52.2	50.5	49.2
	November 1	41.5	40.0	38.8
	Average	43.9	42.0	40.9
Louisiana	March 19	60.8	59.1	57.4
	March 23	53.4	50.7	48.8
	March 31	60.3	57.2	54.2
	Average	58.2	55.7	53.5
	October 11	39.6	36.3	35.0
	October 18	36.2	34.1	32.6
	October 23	27.2	26.1	25.0
	October 30	35.7	34.7	33.5
	November 1	31.0	28.8	26.4
	Average	33.9	32.0	30.5

shucked in the fall striking differences among the groups were apparent. The average percentage of the original weight 60 minutes after shucking was 57.1 for oysters from New Jersey, 40.9 for Maryland oysters, and 30.5 for Louisiana oysters. The difference between the highest and lowest values was 26.6 percent, 8.6 times greater than the difference in the spring. Furthermore, the gradation in percentages observed in the fall bears a relationship to the latitude where the oysters were grown; the further north the habitat of the oysters the less body fluid loss when shucked in the fall.

Stauber (1950) showed the existence of three physiological varieties of oyster from the Bideford River southward to Delaware Bay based on their critical spawning temperatures. Oysters from Chesapeake Bay and Louisiana may represent two additional physiological varieties.

The results obtained with Louisiana oysters agree with the data of Gunter (1942) for Texas oysters. He found that in February and March fewer shell oysters were required to prepare a gallon of shucked oysters than at other times of year, presumably because of seasonal differences in fluid loss.

Louisiana oysters are not as firm and creamy in color in the fall as they are in the spring, presumably because they have "spawned out" during the summer whereas in the spring their gonads are ripening and firm. The body volume of Louisiana oysters shucked during the fall decreased greatly as the body fluid escaped.

CONTROL OF SHELL FLUID

The following experiment was designed to determine the volume of free fluid between the shells of Louisiana oysters and how the shell fluid is controlled. Several oysters were taken from the aquaria and divided into two groups. One group was placed on a table top where evaporation of water from the outer surfaces of the shells could occur rapidly. The second group was covered with wet paper and sheets of plastic material to minimize evaporation of water. When the oysters were divided into two groups the volume in milliliters of free fluid from between the shells of 15 oysters from each group was determined by breaking the hinge and shaking out the fluid. The oysters were then shucked and the weight of the body and escaping fluids were determined. To facilitate comparison of the volumes of shell fluid of different oysters, the values were expressed as milliliters of shell fluid per gram of oyster. The two groups of oysters were kept in the dry and humid atmospheres for up to 24.75 hours. At intervals the volumes of shell fluid and body weights of 15 oysters from each group were determined.

The results are presented in Figure 2. The volume per gram of shell fluid was almost identical in the two groups at the beginning of the experiment. The volume of shell fluid per gram of oyster in the humid evironment remained almost constant throughout the experiment. However, the volume of shell fluid per gram of oysters kept on the table top decreased initially and then became even greater than at the start of the experiment.

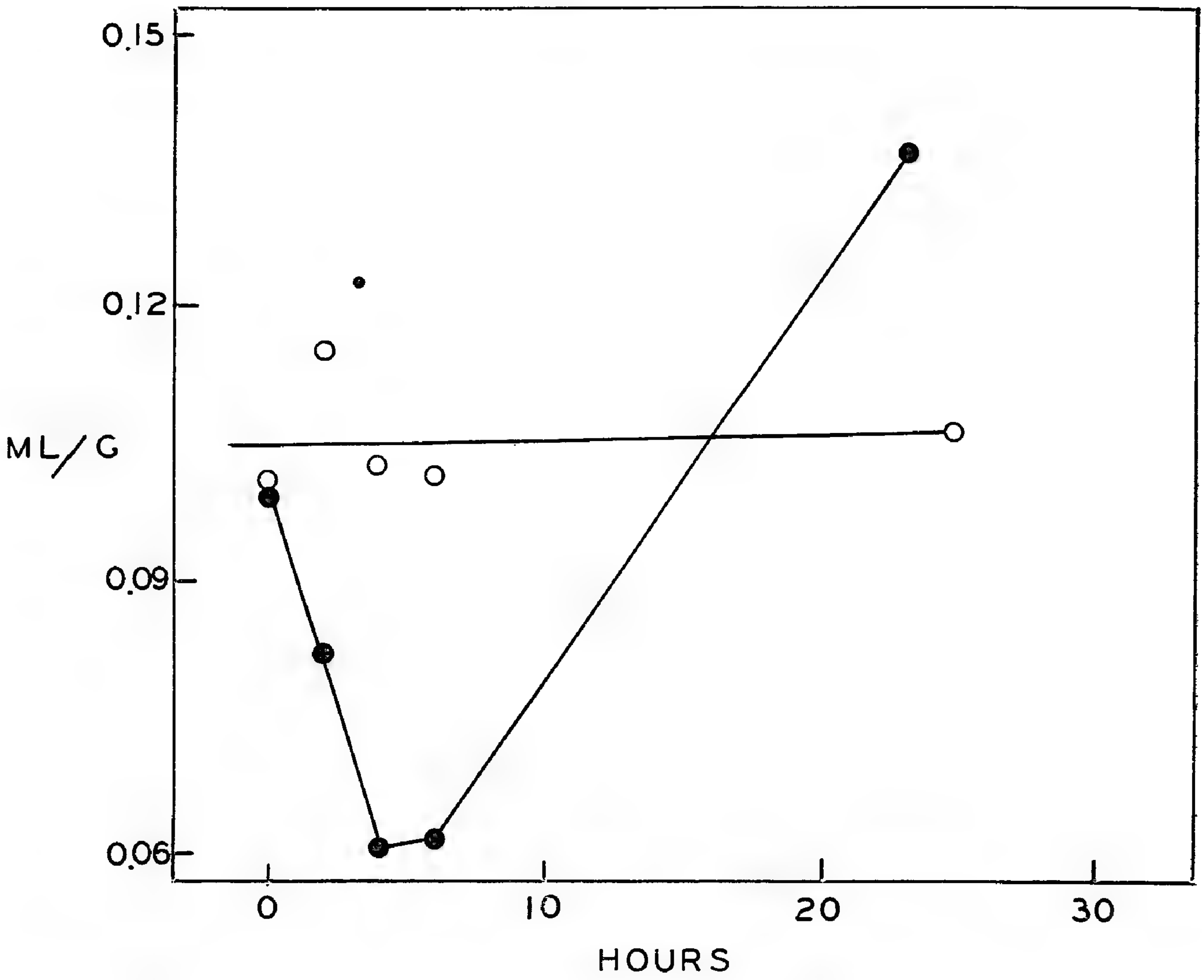

Fig. 2. Volume of free fluid between the shells expressed as milliliters per gram of body weight of oysters in humid (circles) and dry (dots) environments.

In view of this rather unexpected increase, the volume of shell fluid per gram of body weight was determined for 15 additional oysters in the dry environment. The last point on the graph for this group, therefore, represents 30 oysters. The values for the two sets of 15 oysters differed by only 0.024 ml. per gram and were averaged for use in the figure.

Oysters in the dry environment obviously lost fluid from between the shells. The fluid must have been replaced by secretion of fluid from within the body. Fingerman and Fairbanks (1957) determined the losses of body fluids of oysters exposed to high temperature. Heat induced loss of body fluids although no rupture of the body surface was apparent. Oysters evidently are able to secrete body fluid to the exterior but the mechanism is unknown.

CELL COUNTS IN BODY FLUID

The following fluids were obtained from 10 Louisiana oysters; the free fluid between the shells, fluid in the mantle spaces, pericardial fluid, and blood from the ventricle. The number of cells in each fluid was then counted with the aid of a Spencer haemacytometer. The results are presented in Table 2. Considerable individual variation was evident. However, in nine of the ten oysters blood had the most cells and in eight of the ten pericardial fluid had the fewest cells. The percentage of ameboid cells was about the same in each fraction.

TABLE 2

Cell Counts of the Body Fluids of Individual Oysters, Cells/mm.^{3}

	Shell Fluid	Mantle Fluid	Pericardial Fluid	Blood
	950	990	425	1,613
	818	1,392	445	1,564
	871	1,095	379	2,395
	759	973	772	2,316
	317	765	86	910
	284	1,168	56	931
	449	1,122	802	2,406
	211	1,029	59	2,168
	359	445	234	881
	327	1,505	218	1,970
Average:	534.5	1,048.4	347.6	1,715.4
Percentage of Total:	14.7	28.7	9.5	47.1
Percentage Ameboid cells:	20±14	22±13	21±13	23±22

The volume of cells in each fluid, determined in a Wintrobe hematocrit tube, was less than one-tenth per cent, considerably less than reported for the gastropods *Busycon carica, Busycon canaliculatum*, and *Fasciolaria tulipa* by George and Ferguson (1950). Samples of blood of these gastropods contained from slightly less than one percent to as much as two percent cells by volume.

The fact that the internal body fluids, mantle, pericardial, and blood, contain different numbers of cells supports the contention of Fingerman and Fairbanks (1956) that these fractions of the body fluid are physiologically different and that the fluid does not simply circulate from one portion of the oyster body to another.

PROTEINACEOUS AND CHLORIDE CONTENT OF THE BODY FLUID

Oysters were removed from aquaria that contained sea water whose chloride concentration was 219 millimoles per liter. Shell fluid, mantle fluid, pericardial fluid, blood, and fluid from the bladder of the organ of Bojanus were removed from the oysters. Chloride concentration in millimoles per liter and content of proteinaceous material in percentage by weight were determined upon fractions of these fluids. The results obtained from 27 oysters are presented in Figures 3 (proteinaceous material) and 4 (chloride).

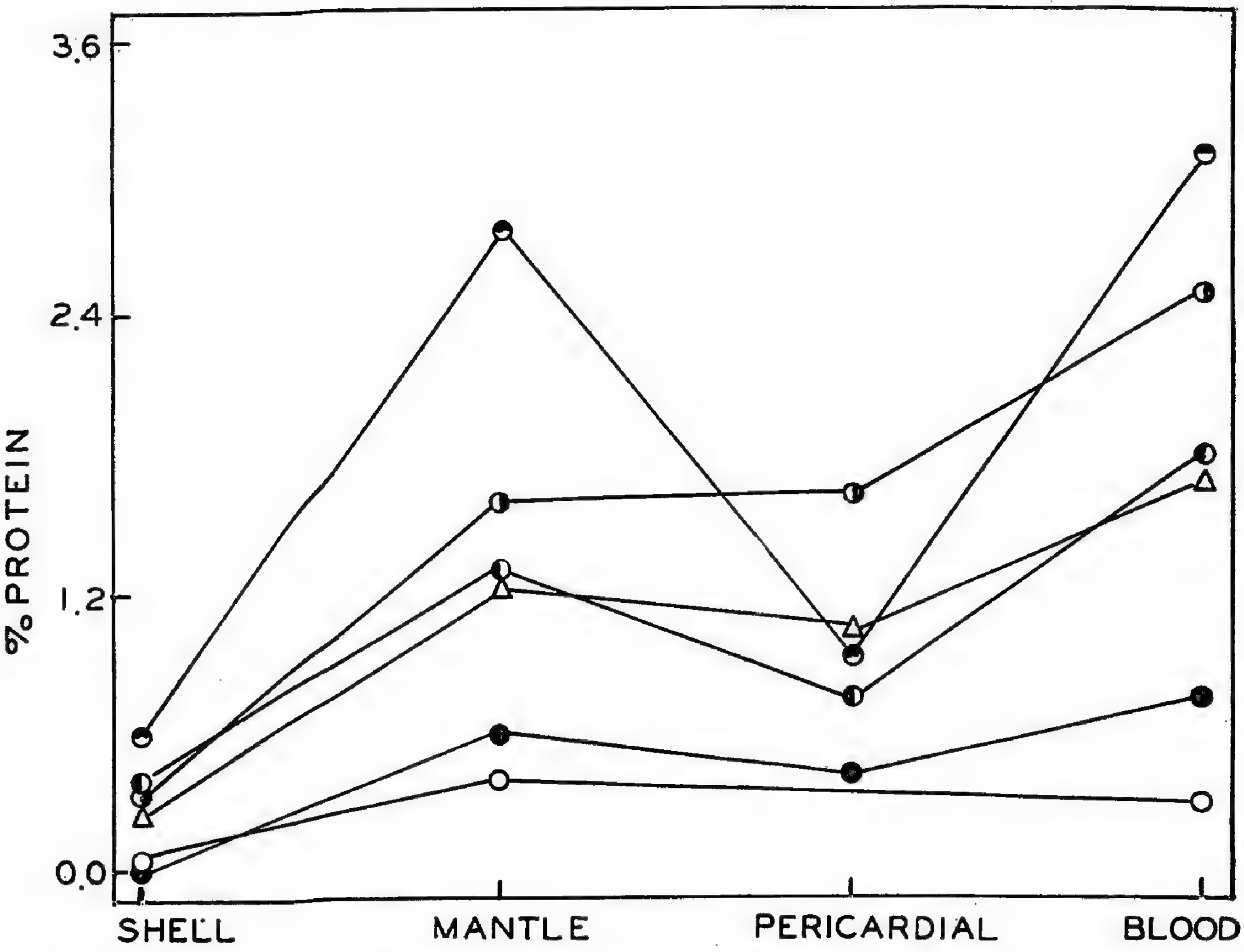

FIG. 3. Concentrations of proteinaceous material in fractions of oysters body fluid. Circles, group 1; dots, group 2; circles with right half filled, group 3; circles with left half filled, group 4; circles with top half filled, group 5. Triangles represent averages for the five groups.

Fluids were divided into five groups on the basis of the concentration of proteinaceous material in the mantle fluid; group 1, 0.00–0.50 percent; group 2, 0.51–1.00 percent; group 3, 1.01–1.50 percent; group 4, 1.51–2.00 percent; group 5, greater than 2.01 percent. As evident from inspection of Figure 3 the concentration of proteinaceous material in the body fluids of oysters was variable just as were the cell counts (Table 2). Shell fluid contained the least and blood the most proteinaceous material.

Similarly, oysters of the different groups showed different chloride concentrations. Some correlation between concentrations of chloride and proteinaceous material was evident. Oysters with greater concentrations of proteinaceous material tended to have greater concentrations of chloride.

The fluids of some oysters contained a greater concentration of chloride than the sea water in the aquaria whereas others contained less chloride. These results are not in conformity with those of Loosanoff (1952) who found that the body fluids of *Crassostrea virginica* were generally hypotonic to their environment. This difference may be due to the different habitats of the oysters; Loosanoff used Long Island Sound oysters. The

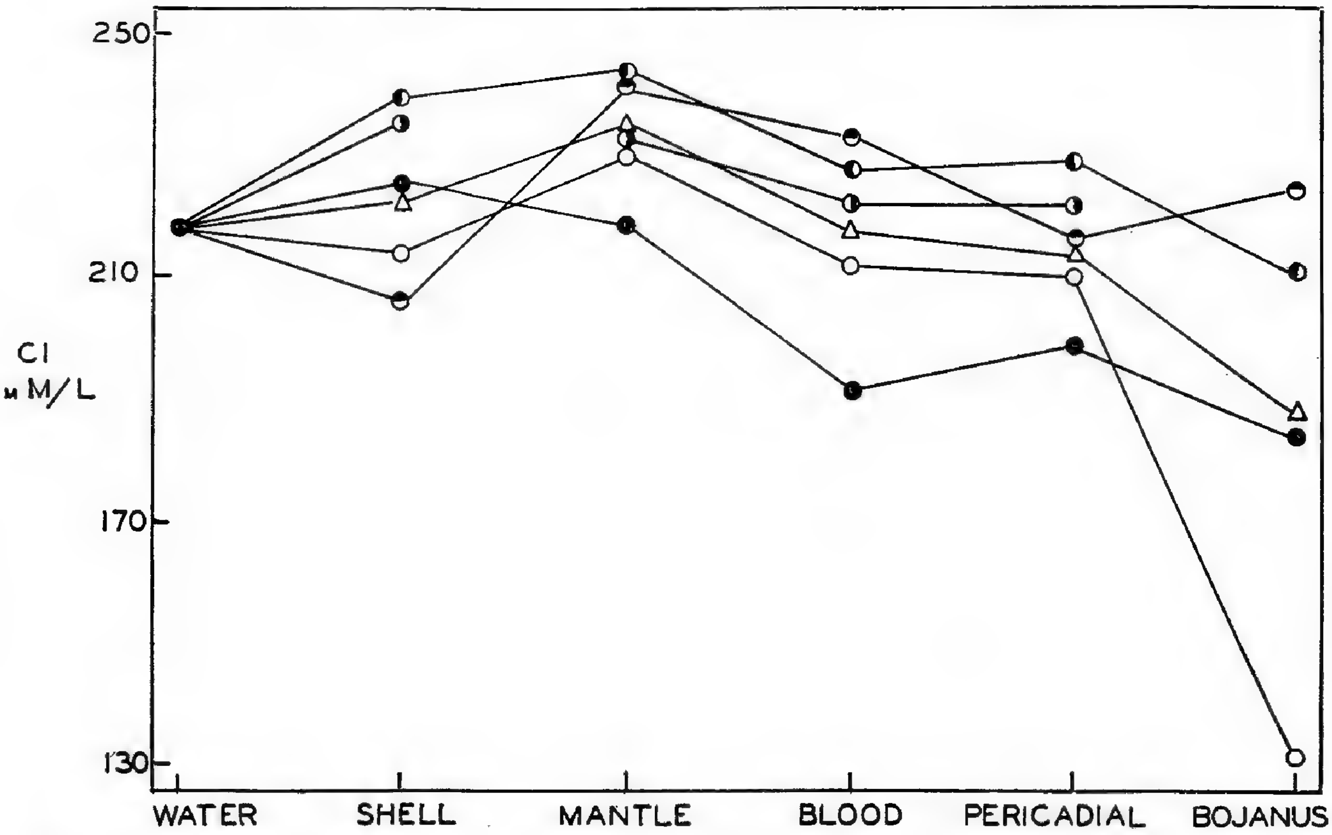

FIG. 4. Chloride concentration of fractions of the body fluid of the oysters used for determination in Figure 3. See Figure 4 for key to symbols.

fluid in the bladder of the organ of Bojanus was hypotonic to the other fluids. Evidently, the kidney functions to conserve chloride when oysters are kept at the salinity used in these experiments.

The data of Figures 3 and 4 also support the contention that the several body fluids differ physiologically. Shell fluid appears to be actively controlled by the oysters and is not simply cells plus sea water trapped between the shells when an oyster is removed from an aquarium.

Summary and Conclusions

1. Body fluid losses following shucking were determined in the spring and fall of 1956 for oysters, *Crassostrea virginica,* grown in Delaware Bay, Chesapeake Bay, and Louisiana. No significant differences between the three groups of oysters were noted in the spring. In the fall, however, Louisiana oysters lost 26.6 percent more body weight than Delaware Bay oysters.
2. Concentrations of chloride and proteinaceous material in fractions of the body fluid were determined. Blood contained the highest concentration of proteinaceous material, shell fluid the least. Mantle fluid had the highest concentration of chloride, higher than found in the aquaria. The organ of Bojanus tends to conserve chloride by secreting a hypotonic urine when oysters are in dilute sea water.
3. Cell counts were made on several components of the body fluid. Blood contained the most cells, pericardial fluid the least.
4. The free fluid between the shells is not simply sea water plus cells. Oysters appear to be able to control the concentrations of chloride and proteinaceous material in shell fluid.

LITERATURE CITED

Fingerman, Milton, and Laurence D. Fairbanks. 1956. Osmotic behavior and bleeding of the oyster *Crassostrea virginica.* Tulane Stud. Zool., 3: 149–168.

————. 1957. Heat death and associated body fluid loss of the oyster *Crassostrea virginica.* Tulane Stud. Zool., 5: 53–68.

George, Wesley C., and John H. Ferguson. 1950. The blood of gastropod molluscs. Jour. Morph., 86: 315–328.

Gunter, Gordon. 1942. Seasonal condition of Texas oysters. Trans. Texas. Acad. Sci., 25: 1–5.

Loosanoff, Victor L. 1952. Behavior of oysters in water of low salinities. Nat. Shellfisheries Assn. Conv. Addresses. 1952.

Nelson, Thurlow C. 1938. The feeding mechanism of the oyster. I. On the pallium and the branchial chambers of *Ostrea virginica, O. edulis,* and *O. angulata,* with comparisons of other species of the genus. Jour. Morph., 63: 1–61.

Schales, Otto, and Selma S. Schales. 1941. A simple and accurate method for the determination of chloride in biological fluids. Jour. Biol. Chem., 140: 879–884.

Stauber, Leslie A. 1950. The problem of physiological species with special reference to oysters and oyster drills. Ecology, 31: 109–118.

Yazaki, Masayasu. 1929. On some physiochemical properties of the pericardial fluid and of the blood of the Japanese oyster, *Ostrea circumpicta,* Pils. with reference to the change of milieu exterieur. Sci. Rept. Tohoku Imp. Univ. (4th Ser.). Biol., 4 (1, fasc. 2) : 286–314.

Note on the Reflex Inhibition of Water Propulsion by the Oyster[1]

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It has very generally been assumed by investigators on the oyster that the water stream through the animal is entirely and only under the control of the ciliary mechanism when the valves are open. Since the water stream through the oyster has played an important role as a physiological index for studies on the behaviour of the oyster, it was thought of importance to call attention to the following observed facts.

To show that at times an inhibitory reflex also operates to completely inhibit water flow through the animal the following observations were made: A small aquarium 8 cm. x 9 cm. x 6 cm. deep was constructed of lucite. An oyster was prepared by mounting it on a small cement support as indicated in Figure 1A. Two methods were used. In the first a toy balloon was used as shown in Figure 1A. In the second procedure shown in Figure 1B, the oyster was prepared by removing, without injury to the tissues, a sector of the upper (right) valve thereby exposing part of the right gill lamella and mantle chamber. A small hole 5 mm. in diameter was drilled between the closed valves opposite the suprabranchial chamber thus making a free path for the flow of the normal stream of sea water through the oyster when the valves were closed A. E. Hopkins (1935). The valves were held closed by means of a rubber band R as shown in Figure 1B. Connection with an electrical drop recorder was made by means of a short rubber tube 5 mm. in diameter fitted into the opening, Figure 1B, G, thus connecting the suprabranchial chamber with an overflow as shown in Figure 1, O. The small aquarium L, with a constant level overflow was supplied with a running stream of sea water.

After an hour of rest the electrical drop recorder was connected for recording on a kymograph. The whole preparation was left in a dark room during the experiments. When an electric light was turned on and off, or better, if the electric light was left on and the mantle was alternately shaded and exposed to light a regular, temporary but complete stoppage of the water current occurred when the light was turned off but never so far as observed, when the light was turned on. This inhibitory response to decrease in illumination could be repeated many times for long periods of time. The light reflex is similar to the closing of the shell by Pecten when similarly illuminated. Mya and Venus also exhibit a reflex retraction of the syphon as studied in great detail in the classical work of Hecht.

Very generally a visible retraction of the gill lamellae accompanied the inhibition of water flow.

Aside from the intrinsic interest in the nature of this inhibitory reflex the facts are cited to show that the control of flow of water through the oyster is not to be assumed as an exclusive control by the ciliary mechanism in the gills of the oyster.

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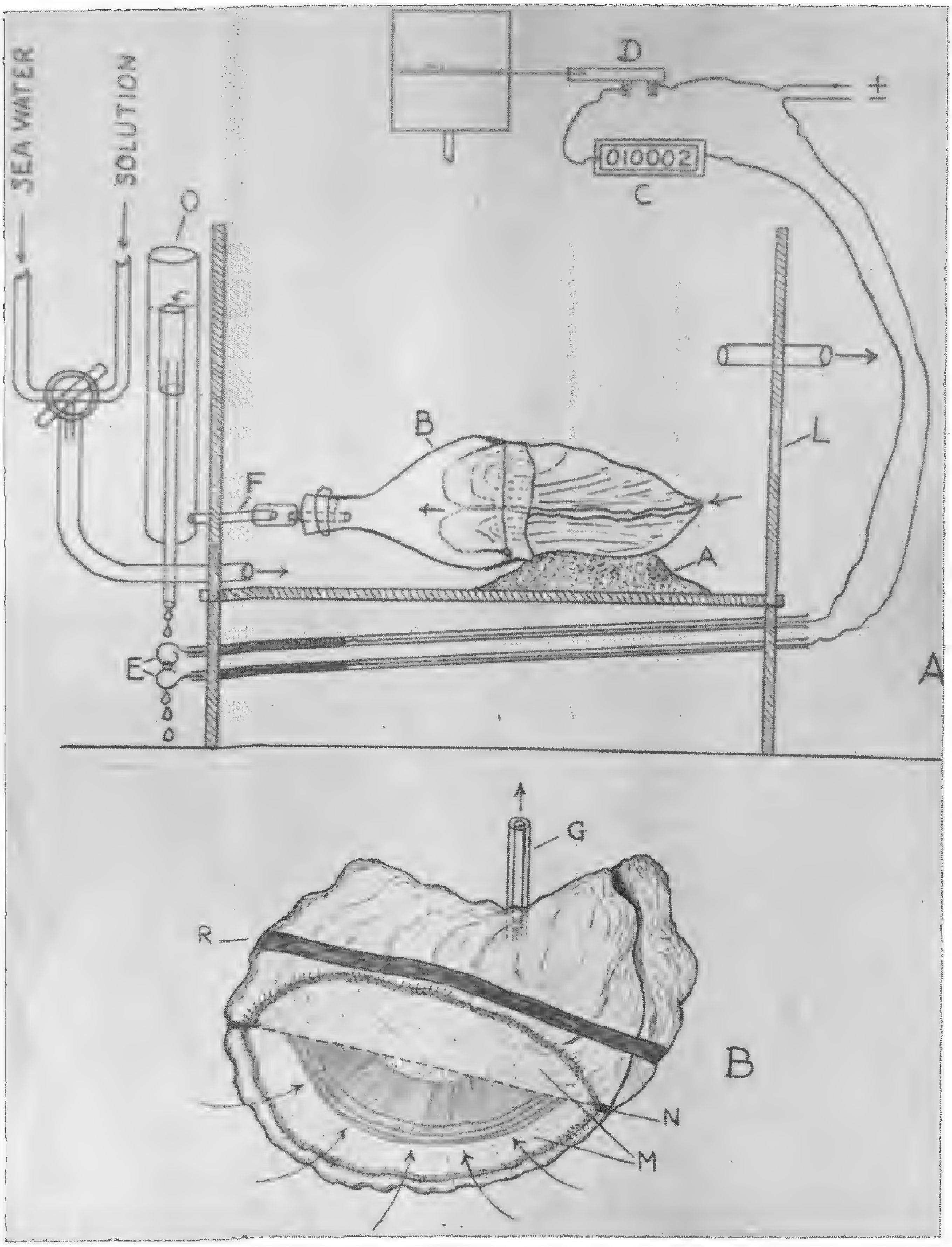

FIG. 1 A. The small aquarium 8cm. x 9cm. x 6cm. deep L is fitted with an inlet through which either the solution to be tested or pure sea water can be admitted. The aquarium is fitted with an overflow. In the first method the oyster is mounted on a cement base A and a toy balloon B is cemented to the oyster shell in the usual way to collect the sea water leaving the oyster. The toy balloon is connected by F to an overflow O. The rate of dropping of the sea water is recorded by means of the electrodes E connected to the counter C and the kymograph recorder D.

FIG. 1 B. In the second type of preparation a sector of the right valve was removed at N exposing the mantle M. The tube G is used when no rubber balloon is employed to collect the excurrent stream of sea water. It is connected directly to the tube F. In this type of preparation the oyster is kept closed by means of the rubber band R, while in the preparation shown in Figure 1 A the valves are free to move in the usual way.

Figure 2 is a sample record showing the temporary inhibition of water flow when the photoreceptors in the mantle region were stimulated by a decrease in illumination. The pumping mechanism is therefore shown to be linked with photoreceptors via the nervous system.

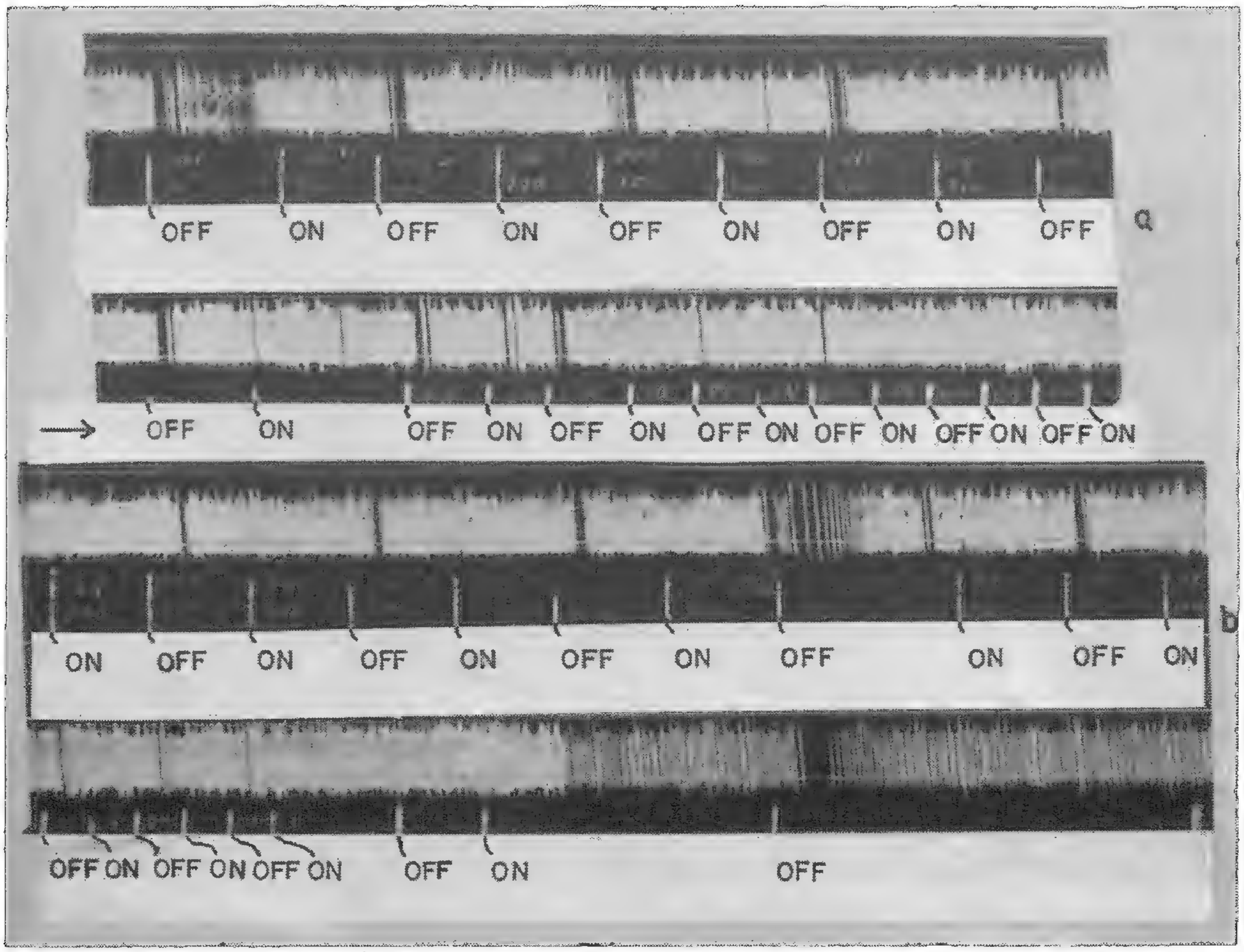

FIG. 2. Reflex inhibition of water pumping by stimulation of photoreceptors in mantle of oyster. Note, decrease in light intensity stimulates, increase does not.

LITERATURE CITED

Hopkins, A. E. 1935. Temperature optima in the feeding mechanism of the oyster, *Ostrea gigas*. Jour. Exper. Zool., 71(2): 195–208.

A Quantitative Study of Clearance of a Turbid Medium and Feeding by the Oyster[1]

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It is a matter of common knowledge to oyster men and investigators on oyster problems that oysters in their natural habitat frequently become covered and often buried by silt deposited after floods from rivers and also as a result of deposits resulting from high winds which cause a shifting of sediments from adjacent bottom. If such deposits are not removed by wind and wave action within a matter of a few hours or days the oysters die. It is also common observation that in some normal habitats of the oyster the supporting substratum is continually or intermittently kept free from deposit by the rapid flow of water currents over the oyster bed produced by tides and to a lesser extent by wave action. In oyster habitats of the latter type it would appear that the tendency to deposition of sediment would be of little or no significance.

In what follows we shall consider in detail the relation of the bahaviour of the oyster to the turbidity of the medium and finally the question of the oyster as a contributor to the process of silting on certain types of oyster beds. The possible consequences of self-silting of an oyster bed by the oyster has so far as the writer knows never been investigated and only considered briefly for Cardium by a single investigator, Damas (1935).

Turbidity of Sea Water and Food Selection by the Oyster

Since the relation of the oyster to turbidity of the sea water medium is an extremely complicated matter it will be profitable to formulate and outline the basic facts and

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phenomena which enter into this complicated problem. In sea water of practically any location the particulate components of the suspension causing turbidity may for our purposes be conveniently classified as follows:

- (a) Organic (containing available potential energy)
    - (1) Detritus—derived from dead plants and animals
    - (2) Living organisms (micro-plankton)
- (b) Inorganic (mineral having no available chemical energy)
    - (1) Fine colloid suspensoids which tend to remain in suspension
    - (2) Coarse suspensoids which readily settle out by the force of gravity

It is obviously important to remember that the oyster is subjected to enormous changes in the composition of the suspension within the above classification. For our present purposes we shall omit from consideration turbidity which at times is caused by suspensions of larger organisms such as copepods, etc., which in any case so far as known do not constitute a part of the regular food supply of the oyster. So far as at present known there are two and only two possible sources of energy available for metabolism of the oyster. These are represented by the types of materials under (a) in the above classification. Since the energy requirements of the oyster can only be derived from these organic components then the alternative conditions which confront the oyster are first, that all components be taken in proportion as they occur in the suspension, with digestion of those which are suitable and possess energy value. This requires no external food selecting mechanism. The second condition is that the oyster be able to select all or certain ones of the organic or inorganic components of the suspension. This would require a highly specialized and effective mechanism of selection of food. The third possibility—which is that actually observed in the oyster—is the partial separation of organic and inorganic components depending upon external and internal conditions of the oyster. This requires a partial food selection process (Lotsy, 1893; Kellogg, 1915; Grave, 1916; Nelson, 1923; Yonge, 1926; Loosanoff and Engle, 1947; Loosanoff, 1949).

One of the purposes of the present investigation has been to develop methods which make possible quantitative measurement of the efficiency of the mechanism of food selection in the oyster, under a variety of conditions both external and internal to the oyster.

The Clearance Function of the Oyster

It is a remarkable fact of common knowledge to oceanographers that everything in particulate suspension is ultimately precipitated from sea water thus making it possible for the force of gravity to bring about deposition of the material. To date after numerous attempts we have completely failed to find any simple substance which will form a stable suspension in sea water. In order to indefinitely maintain a particle in suspension, force or energy must be supplied to support the particle. For example, mechanisms include kinetic energy of a particle in Brownian movement, electric charge on the particle, or self-motility of living micro-plankton. Mechanisms are needed to keep such floating substances as oil of lower density dispersed in the sea water medium as well as to prevent deposition of particles on the bottom.

The rate of fall of particles above colloidal dimensions in sea water as in other liquid media is governed by the well-known Stokes law as modified by Einstein. This law is fundamental as the starting point in all studies of turbidity which involve deposition of particles from a suspension by the force of gravity. From this it will be evident that the disappearance of turbidity in sea water in the presence of the oyster will be dependent upon (1) removal of particles by gravity and, (2) the removal of particles of the suspension by the oyster itself. The remarkable fact which is observed when a healthy active oyster is suspended in turbid sea water having a mixed suspension of organic and inorganic particles is that the oyster is practically always able to clear the medium completely causing the transparency of sea water to approach very close to that of distilled water. The *limits* of the functional capacity to which the oyster is capable of decreasing the turbidity of very fine colloidal material in very high dilution in sea water is a special problem requiring methods of measurement different from those used in the following experiments. It should be emphasized that the normal oyster is enormously more efficient in clearing ordinary turbid sea water than is gravity. The difference is readily determined by comparing the rate of decrease in turbidity in a container with an oyster with that in an equal volume of the same sea water in which clearance takes place by gravity.

The clearance by an oyster of a weak milk suspension in sea water is illustrated in Figure 1. The difference between the rates of clearance of a suspension of fuller's earth in sea water by the oyster and by gravity alone is illustrated by the curves A, B and C in Figure 2. Each of the curves A and B represent the rates of clearance by four oysters in each of two separate vessels, each vessel containing 9 liters of sea water to which was added 150 cc. of a strong suspension of fuller's earth. Curve C shows the simultaneous rate of clearance by gravity of a duplicate without oysters. The approximate rates of clearance by the four oysters are found by subtracting curve C from each of the curves A and B. That this is only an approximation is due to the fact that clearance by the oyster is accompanied by turbulence while the corresponding clearance in the duplicate by gravity does not involve the effect of turbulence.

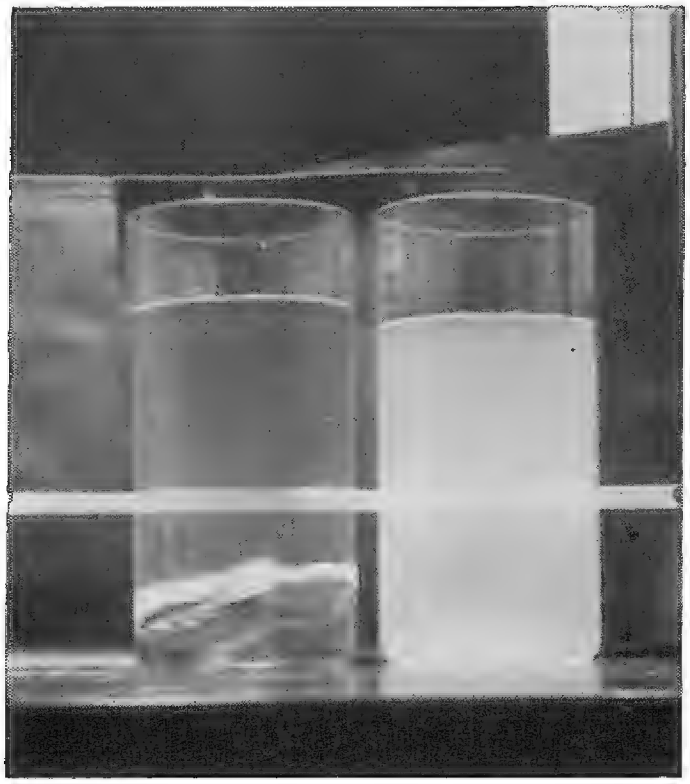

FIG. 1. Clearance of a suspension of 5 cc milk in 3 liters sea water. A. Container with oyster after six hours. B. Control without oyster.

From facts which have been established by various investigators (Kellogg, 1915; Yonge, 1926), it has been shown that filtration by the oyster depends upon the operation

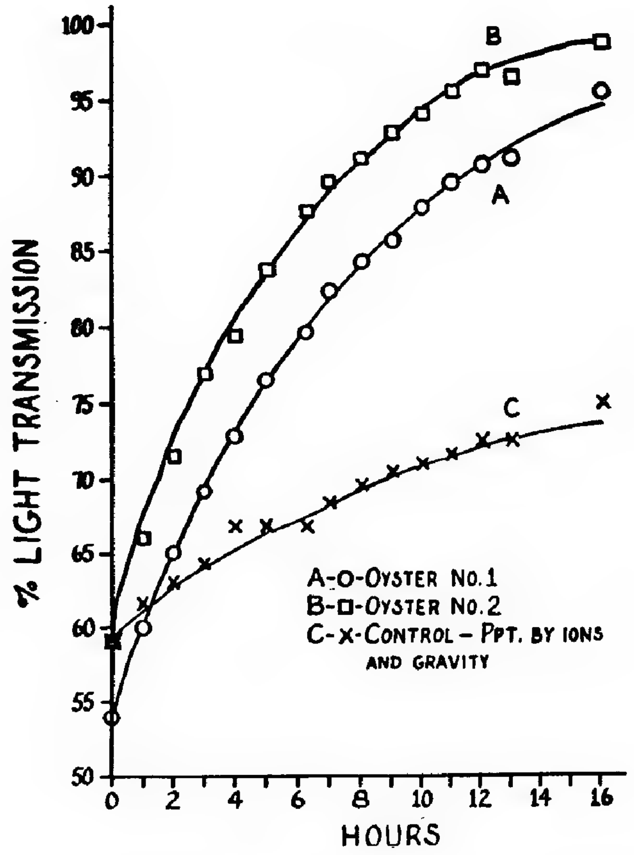

FIG. 2. Clearance curves. See text for explanation.

of the ciliary mechanism of the gill filament. The filament is at least in part under the control of the nervous system. Further evidence for this reflex control was presented in a preceding paper. The other part of the mechanism of filtration which is not dependent upon ciliary 'porosity' of the gills is the removal of particles by specially effective wetting properties of the mucous secretion formed by the gills, palps and mantle.

All particles which are removed from the medium either (1) pass back out into the medium or (2) pass into the mouth. As yet little or nothing is known definitely as to whether or not there is complete removal of all suspended particles including those of very small colloidal dimensions. ZoBell and Landon (1937) found that the California mussel removed 99.9 per cent of all bacteria added to sea water.

Types of turbid media which can be cleared by the oyster are, suspensions of yeast, milk, kaolin, carbon black, fuller's earth, yolk of hen's egg, soluble starch, and various inorganic suspensoids such as calcium carbonate, etc. Clearance of suspensions of isolated chloroplasts and microorganisms such as *Euglena*, *Chlorella*, diatoms, and protozoa has been observed.

An important contribution to the problem of clearance by the sea mussel *Mytilus californianus* is that of Fox, Sverdrup and Cunningham (1937). These investigators determined the rate of clearance of calcium carbonate suspensions by the mussel in aquaria or cylinders containing known volumes of sea water suspensions. This procedure, like that illustrated in Figure 1, we shall designate as clearance in a *closed* system, in contrast to the clearance by the oyster in the experiments to follow in which the oyster operates on a directed continuous stream of sea water of known and predetermined dimensions, volume and velocity. The latter we shall designate clearance in an *open* system.

In their more precise experiments Fox, Sverdrup and Cunningham (1937), allowed the mussels to clear sea water suspensions of known quantities of calcium carbonate in a closed system. The rate of clearance was followed by making quantitative determinations of the calcium remaining in suspension as calcium carbonate. Correction was made for the calcium in sea water used as the medium for the calcium carbonate suspension. The results of their experiments strongly indicated that the California mussel in all probability removed completely all of the calcium carbonate particles in the sea water which at any instant passed through the gills. The amounts of suspended calcium during clearance were expressed as an exponential function of time so that the amount of calcium carbonate removed by the mussel in unit time was proportional to the total amount of calcium carbonate suspended at that instant. They applied the exponential equation

$$p = p_o e^{-\left(\frac{nm}{M} + a\right)t} = p_o e^{-bt}$$

where p equals suspended calcium in milligrams per liter.

p_o = amount of suspended Ca in the closed system at the beginning of the experiment
n = the number of mussels in the vessel
m = volume in liters pumped by one mussel in unit time
M = volume of sea water in the vessel
t = time and
a and b are logarithmic decremental constants determined from the experiments.

On the above assumptions and under the specified conditions in the *closed* system this enabled them to calculate the volume of sea water pumped by the mussel in unit time by means of the equation

$$m = M \frac{\quad}{n}$$

This method has a strong appeal to any investigator who appreciates its elegance and simplicity. However, in practice, owing to the diversity of changing factors in the processes of clearance by the oyster, and the labor involved in making numerous chemical analyses, direct measurement of the turbidity (per cent light transmission) of the suspensions by the Fisher electro-photometer used as a turbidimeter, offered a simpler and rapid approach to the problems of clearance by the oyster.

Methods

In order to determine quantitatively the various factors which enter into the clearance process it became necessary to control and measure separately the volumes of the material passing through the alimentary canal of each oyster in any one experiment as well as the corresponding volumes of rejecta from the gills in the same oyster. In this way it became possible to follow quantitatively the clearance process *simultaneously* with that of feeding and rejection. Furthermore, this made it possible to obtain a quantitative measure of the efficiency of food selection and its variations in the oyster. It is important to note that determination of the volume of faeces is the only quantitative way in which the equivalent volume intake of food in an oyster can be accurately measured. Another important index of feeding and selection which now becomes available

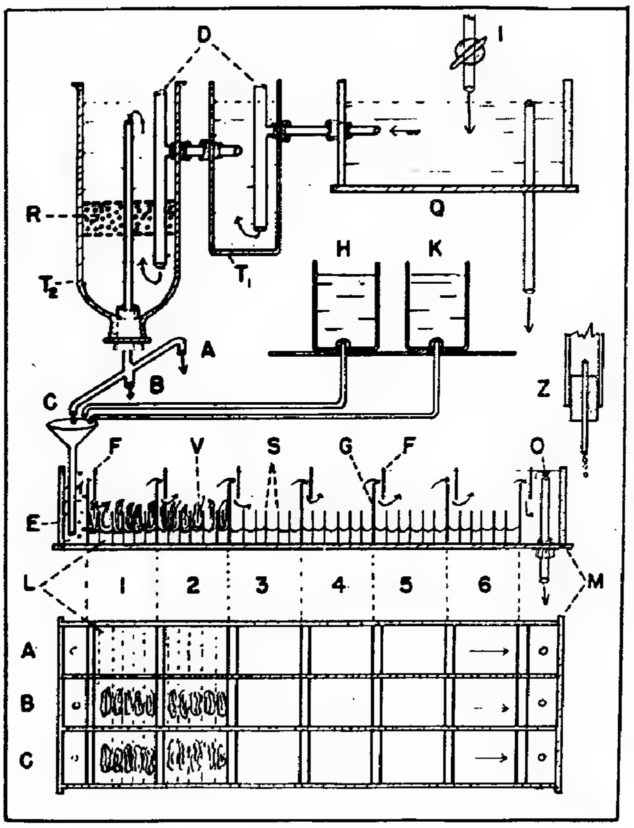
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FIG. 3. Apparatus. See text for explanation.

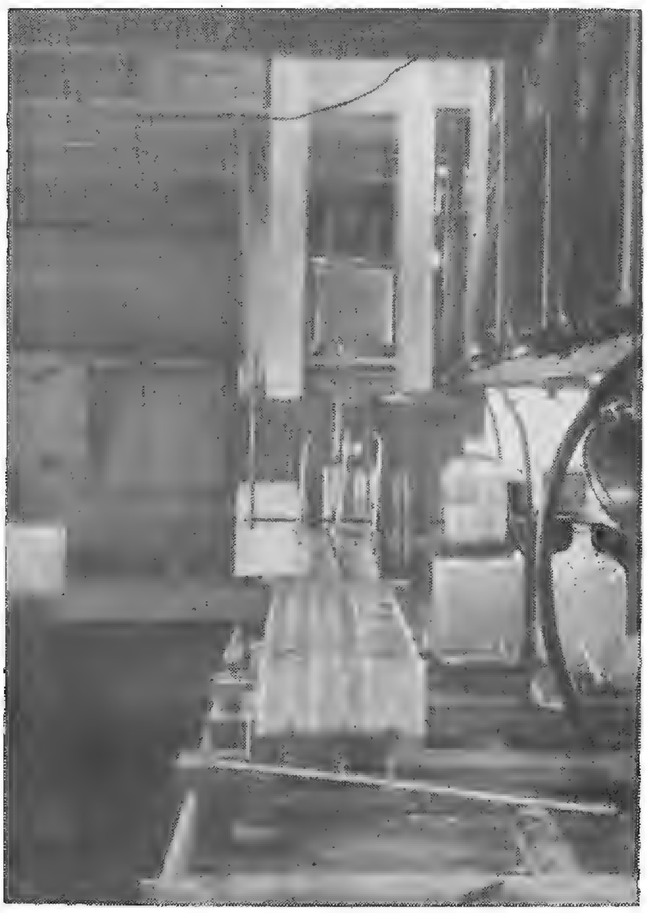

FIG. 4. Lucite apparatus. See text.

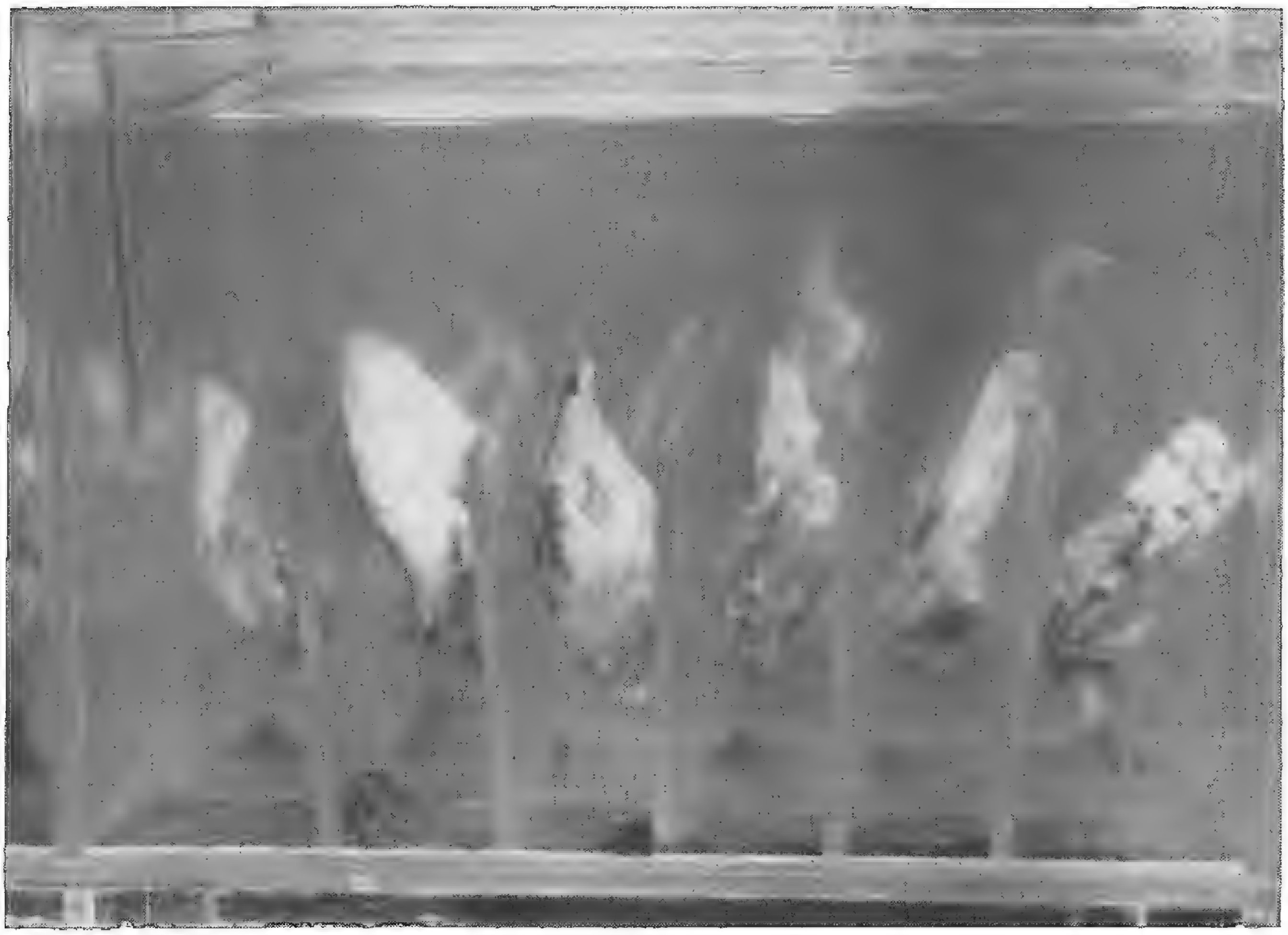

FIG. 5. Oysters in gradient trough. See text.

for quantitative study is the ratio $\left(\frac{\text{vol of rejecta}}{\text{vol of faeces}}\right)$ or simply $\frac{P}{F}$. Furthermore the methods to be described will make these two components available for the application of quantitative methods of mechanical analysis similar to those used in studies of soils.

The apparatus was constructed of glass and lucite as shown in Figures 3 and 4. The sea water, pumped directly from the Pass, at Port Aransas, was supplied continuously through I to the constant level tank Q. T_1 and T_2 are glass containers of 7 and 12 liters capacity respectively. These, along with the constant level aquarium Q, serve as sediment traps. T_2 also contains a removable cotton filter R. This filter removed all suspended micro-plankton of the dimensions of diatoms from the sea water stream. The outlets A, B, and C supply each of the correspondingly labeled sections, A, B, and C of the trough at the bottom of Figure 3. The velocity of flow is maintained constant by the fixed head between Q and outlets A, B, and C. Difference in volume and velocity of flow is fixed and regulated by the use of glass tubes of equal length and different diameters shown in Z. To indicate the constancy of velocity of flow obtainable, a beaker of 1170 cc. capacity was filled three different times during one hour in 1′25″, 1′27″, and 1′26″, respectively. This constancy can be maintained from day to day if the supply tubes are kept clean. Glass aquarium H and additional ones which can be added contain the food suspension of chloroplasts or diatoms which may be supplied as food at a known rate of flow. K is a similar constant level (not shown) supply of fuller's earth or other inert suspension. Both H and K are supplied with motor stirrers (not shown) to maintain homogeneity of the suspensions. Food suspensions mixed with different controlled amounts of inert suspensions may therefore be supplied to each of sections A, B, and C. Section A is usually used as a blank without oysters to determine the volume of sediment which settles out by gravity during any experimental period. This may then be applied as a correction to each of the corresponding compartments 1 to 6 of sections B or C as required.

Continuous aeration is made ample and equal by turbulence in each of the funnels C. All air bubbles at E are prevented from entering the sections by the baffle F. Uniform mixing in each of the compartments 1 to 6 is provided by a system of glass baffles F and G. Each of the compartments 1 to 6 of sections A and B hold 6 oysters all oriented umbo down so that all faeces of each oyster fall into the same side of the section and all psuedo-faeces fall into the opposite side of that section. Separator plates S made of ⅛ inch thick lucite separate completely both the faeces and psuedo-faeces of each individual from those of the adjacent oyster, Figures 3 and 5. Thus a complete determination may be made of the volumes of faeces and psuedo-faeces produced by each individual oyster. Since there are 6 compartments each containing 6 oysters the results obtained simultaneously, are based upon 36, 72, or 108 oysters, depending upon the type of experiment. Since the oysters in each one of the series of 6 compartments operate in succession on the same volume and velocity of the stream, the turbidity is successively reduced in amount from compartment 1 to 6. The turbidity or sedimentary load is determined at the entrance of compartment 1 and at the exit of compartment 6 together with the volume flow. The total quantity of suspended material removed by the oysters in a section may be determined, after correcting for sedimentation by gravity as found in Section A. Experience has shown that the correction for gravity in sedimentation under the conditions of the experiment is often negligible, depending upon the kind of suspensions used.

The photographs Figure 4 and 5 show the general view of an experiment in which the volumes of faeces and psuedo- faeces produced by each individual oyster were being determined under conditions of constant volume flow and a known mixture of chloroplast suspension and fuller's earth in the sea water stream. The progress of clearance of the constant stream of sea water passing through each of the sections A, B and C is determined as per cent light transmission at the entrance and exit, or if necessary in each of the 6 compartments. Such a typical turbidity gradient is shown in the curves in Figure 6, where curves B and C are gradients of turbidity in sections B and C, containing oysters, and curve A is for the control section A, without oysters.

The Ratio, $\left(\frac{\text{Volume of P}}{\text{Volume of F}}\right)$ and its relation to Turbidity

To illustrate this relation the results of the following experiment are given. A constant stream of sea water flowing at the rate of 565 cc per minute was delivered to each one of the sections A, B and C, Figure 3. The unfiltered sea water which came directly from the Pass had a salinity of 23.5‰, temperature 26.8° to 27.4° and a turbidity at the entrance of compartment Number 1 which varied from time to time between 66.6 per cent and 92 per cent (= 13 parts per million to 6 p.p.m.) transmission during the experiment. The duration of the experiment was 64 hours. Thirty oysters were placed in each of Sections B and C. Section A was left as a blank to determine the volume of sediment deposited by gravity. At the end of 64 hours the castings and rejecta were collected separately in each of the 6 compartments (5 oysters in each compartment) of Sections B and C and placed in graduated 50 cc cylinders. The deposits, due to gravity, in each compartment of Section A were collected in a third set of 50 cc cylinders. Since Sections B and C were duplicates, each containing the same number of oysters and other conditions being identical, the castings and rejecta respectively of correspondingly numbered compartments were mixed and set aside to settle for five hours in the cylinders. Deposits from Section A were treated similarly. A photograph taken at the end of 5 hours is shown in Figure 7. The left hand cylinder containing rejecta from compartments B 1 and C 1 is a 100 cc graduate and therefore the comparable height of the column in this cylinder *should be approximately twice as high as shown.* The relative volumes of rejecta P and castings F produced in 64 hours from the normal sea water of the open Pass, of variable turbidity, are shown in the graphs of Figure 8. Volume readings were taken after 5 hours settling of the suspensions.

In spite of the fact that these two duplicate sets, of 30 oysters each, operated on a variable and complex natural sea water suspension, the deposition by the oysters in each successive compartment diminished at a decreasing rate. The volume of castings (equivalent to volume of food intake) as well as the volume of the rejecta diminished uniformly. The ratio of volume of rejecta to the volume of castings $\frac{P}{F}$ diminished from 4.44 to about 2 (Figure 7). The successive decreases in volumes of deposits of both rejecta and of food equivalent are dependent upon the decrease in the concentration of the suspension in the 6 successive compartments. The effect of decreasing turbidity on the rate of clearance by the oyster is shown in curves A and B, Figure 2 in a *closed* system. Furthermore the same relation between decreased rate of formation of both castings and rejecta was demonstrated repeatedly in other experiments in which fuller's earth was added at the intake of Section B in order to increase the initial turbidity in B over that in Section C. The experiments show that the volume of the intake by mouth is *relatively* greater at low turbidities (low concentrations) than at higher turbidities. This range is represented by an equivalent turbidity range of approximately 30 p.p.m. down to 5 p.p.m. of fuller's earth suspension. Another important fact to note is that under the conditions of the experiment the capacity of the oyster as a depositor of sediment even in this low range of turbidity of sea water is as much as *fifty* times greater than gravity. Under certain conditions on natural oyster beds this fact as we shall see in a following paper may become of special importance. The relative composition of rejecta and castings in each compartment of Sections B and C in such experiments will be considered below.

The Ratio $\left(\frac{\text{Volume of P}}{\text{Volume of F}}\right)$ as a Function of Velocity of Unidirectional Flow

Sections B and C of the troughs shown in Figure 3 were each filled with 30 clean oysters averaging 2 inches in length and having no external parasites. The sea water was pumped as usual directly from the Pass and had a range of variation of turbidity of 80 to 95 per cent during the 44 hour test. This represented a turbidity of 20 p.p.m. down to 3 p.p.m. of suspension of standard fuller's earth in sea water. Ordinarily this would be considered relatively clear sea water. The only difference in the conditions in Sections B and C was that velocity of flow (and therefore rate of volume change) in Section B was five times the velocity in Section C. The results are given in Table 1 and show that under the conditions of the experiment a fivefold increase in velocity approximately doubles both the volume of food intake and the volume of rejecta. The *overall* ratio of $\frac{P}{F}$ (column 8) remains at about 2 at this range of turbidity. In other experiments where the average natural turbidity was higher this overall ratio was increased to approximately 4. This is to be expected from the facts shown in the curves of Figure 8 in which, as the turbidity increased, the ratio $\frac{P}{F}$ also increased. The experiment shows that other factors being the same, increase of velocity of flow of a natural sea water suspension increases the volume of *both* rejecta and food intake by the oyster. In another ex-

TABLE 1

The Range of Variation of Turbidity of Sea Water During the Experiment at Entrance of Sections B and C was 80–95% Transparency Equivalent to 20 to 3 p.p.m. of Standard Fuller's Earth Suspension

1	2	3	4	5	6						7	8
Duration of Test Hrs.	Volume of Flow	Relative Volume Flow	Section	Deposit	Compartment Number						Total Volume of Deposit cc.	Ratio $\frac{\text{Total Vol. P}}{\text{Total Vol. F}}$
					1	2	3	4	5	6		
44	2600	5	B	P	23.5	18.0	12.0	13.0	16.0	9.5	92.0	2.2
				F	10.5	7.5	6.0	5.0	6.5	5.0	40.5	
44	520	1	C	P	19.0	11.0	8.0	4.0	3.0	2.0	47.0	2.0
				F	7.5	4.5	3.5	3.0	2.5	2.0	23.0	

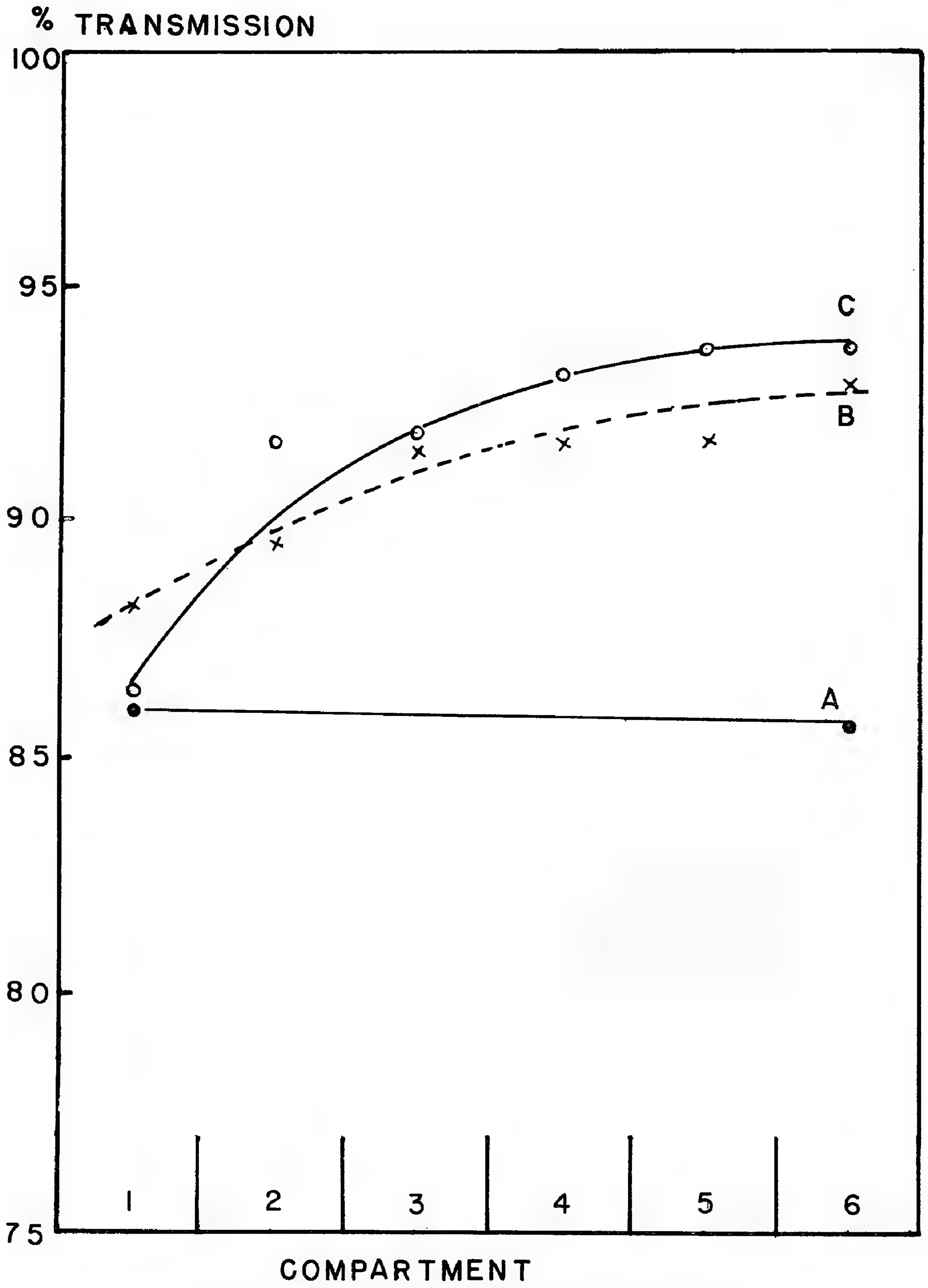

Fig. 6. Transparency in the chambers of the trough. See text.

periment a fourfold increase in velocity of flow more than doubled the volumes of both the food and the rejecta. To show the quantitative interrelations of the effects of velocity of flow and turbidity requires more extensive experiments.

It must be noted that it is the velocity factor which is of primary importance in these experiments since the cross sectional area is fixed and equal in all sections, B, C, and A.

Possible Application of These Results to Conditions on the Oyster Bed

The experiments show that at these low turbidities increase in velocity of flow over the oyster becomes of increased importance in determining the volumes of both the food intake and the rejecta. From this it is to be expected that relative stagnancy of sea water having a low concentration of food content over an oyster bed may seriously limit the food intake by the oyster. On the other hand such low food content (low turbidity) may be ample if the movement of sea water is rapid. A low velocity of flow would be expected to become a limiting factor over the central areas of thickly populated oyster beds. Sluggish water movement and low concentration of food suspension over an oyster bed would result in the greatest growth and development of the oyster bed at its periphery. Furthermore, an elongated form of an oyster bed with its long axis placed at right angles to the direction of flow would increase the effectiveness of feeding by the oysters, other conditions being the same. The advantage if any to the oyster bed would be most marked at low concentrations of food particles.[2]

The design of the experimental trough in Figure 3 readily shows the effect of crowding of oysters, a problem of practical importance. Overcrowding on the oyster bed can be readily shown by comparing (a) the clearance in compartments 1 to 6 in one section each containing one or two oysters, compared to (b) the clearance when each compartment is crowded with 6 or more oysters. Similarly, the volume of feces and rejecta may be simultaneously determined. All other conditions in Sections B and C must be maintained identical throughout such a test.

Individual Variation in the Behavior of the Oyster and Its Importance in Experimentation

In most types of accurate experimentation the oysters used must be completely free from external parasites and commensal organisms. Since the oyster is one of those organisms which generally harbors an unusual array of external and internal parasites, and commensals, oysters from natural beds are often not dependable material for critical experiments. The oysters used in the final experiments had therefore been grown from selected spat in protected wire baskets placed above the bottom in a favorable field location for growth. In spite of such precautions the oyster which is perfectly clean externally usually exhibits a wide individual variation in behavior from time to time. Numerous past investigators of the oyster do not appear to have fully realized the extent of variability of the feeding behavior of an apparently uniform group of oysters. Such information on variability always contributes to sound judgment in the evaluation of experimental results. Eighteen oysters of uniform size from a lot of 400, each about two inches in length, were selected at random. These oysters were shipped from Barataria Bay, Louisiana, to the Marine Institute at Port Aransas. They had been grown from spat and were free from observable external parasites and commensal organisms. They had also been left to adjust to salinity and other conditions at the Institute Laboratory for nearly two months, and during this time showed some growth.

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[2] After this had been written, Dr. Sewell Hopkins called my attention to publications by C. Grave (1901, 1905) in which field observations of the form and orientation of the oyster beds in North Carolina actually agree with the predictions made on the basis of the above experiments.

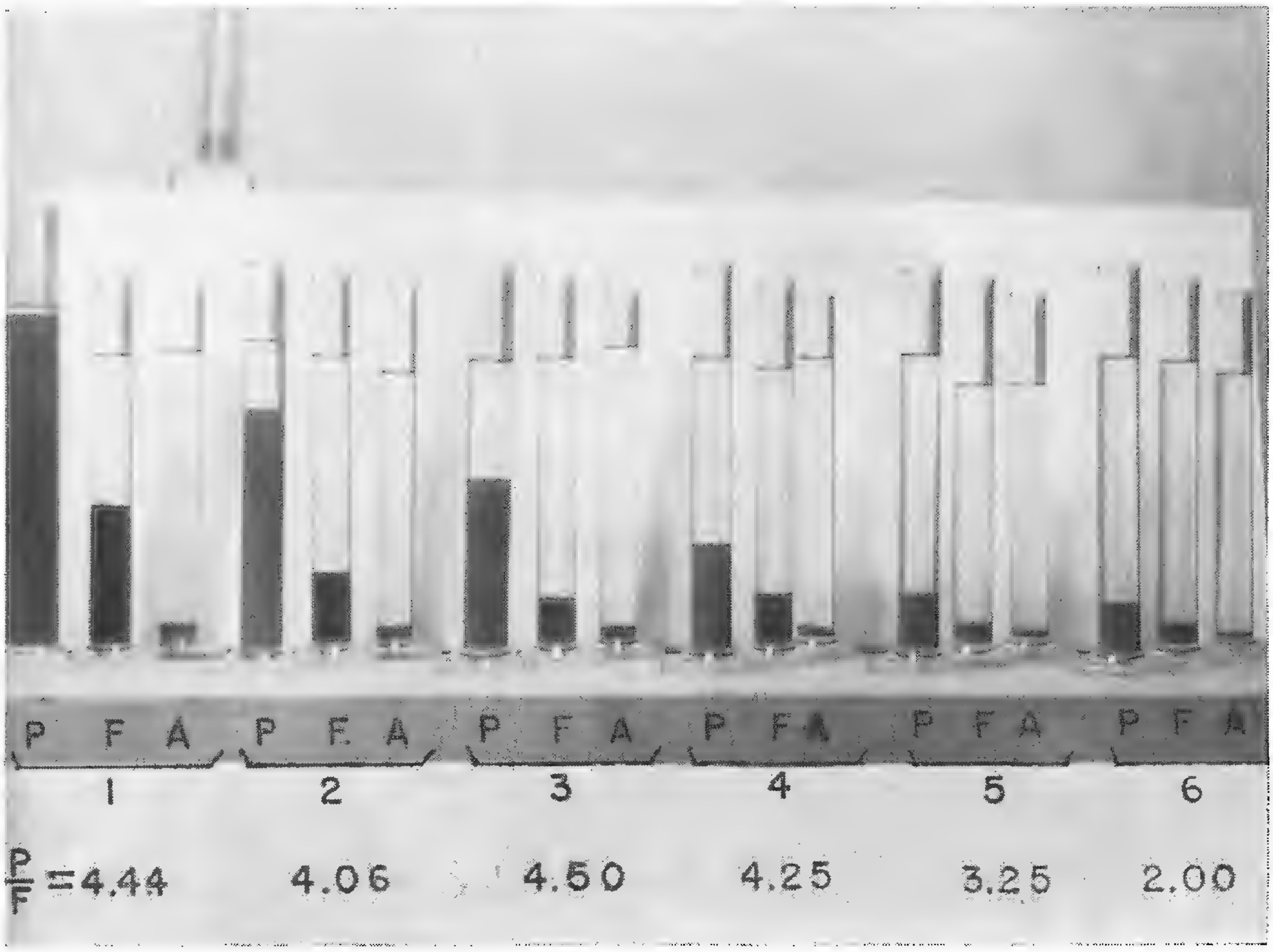
P F A P F A P F A P F A P F A P F A
1
2
3
4
5
6
P/F =4.44
4.06
4.50
4.25
3.25
2.00

FIG. 7. Pseudofeces (P), Feces (F), and gravity silting (A) in the chambers of the trough gradient. See text.

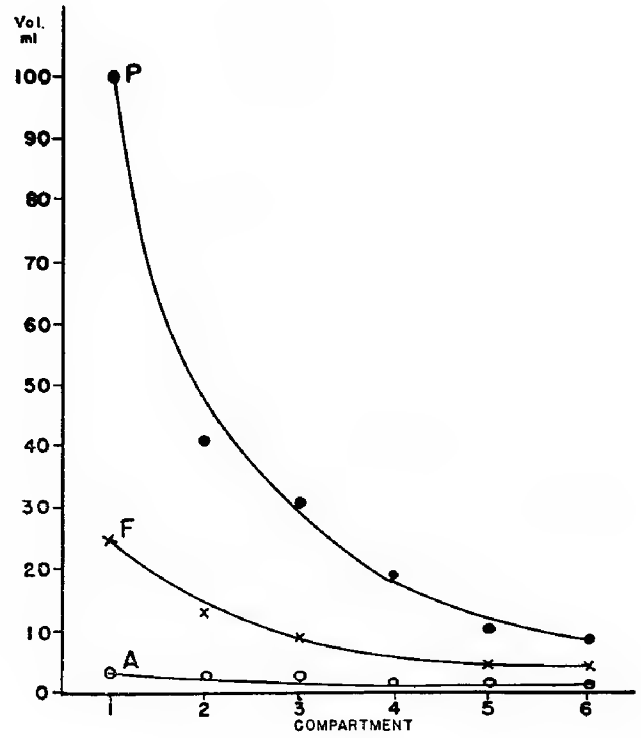

FIG. 8. Silting in the trough gradient due to Pseudo-feces (P), Feces (F) and gravity (A). See text.

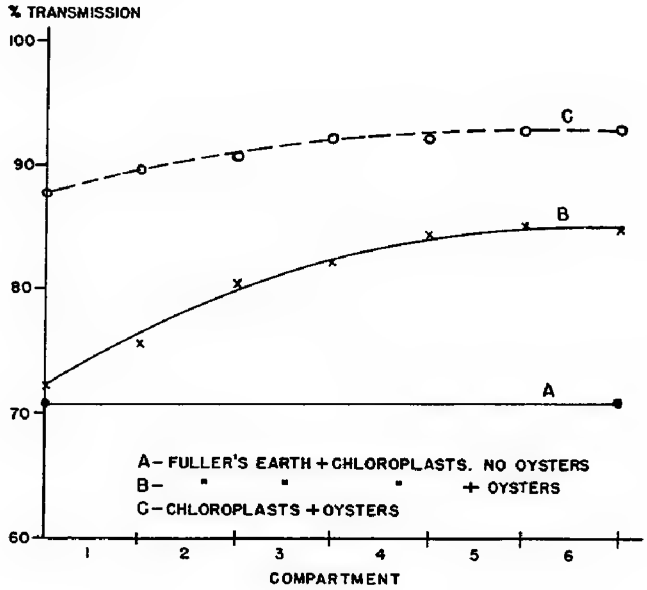

FIG. 9. Clearance of suspensions containing mineral and food components in the trough gradient. See text.

The 18 oysters were placed in Section C and arranged in three rows of 6 each in compartments numbers 1, 3, and 5 of Figure 3. A rapid, constant stream of fresh unfiltered sea water flowing at a rate of 1 liter per minute was passed through the section. The transparency during the experiment was between 86 and 92 per cent transmission, a relatively low range compared to distilled water taken as 100 per cent.

There were two test periods, the first period of 48 hours and the second period of 22 hours, Column 2, Table 2. At the end of each period the faeces and pseudo-faeces produced by each oyster was carefully collected in graduated 15 cc. centrifuge tubes and allowed to settle for four hours, at the end of which time the volumes were recorded. All the data are summarized in Table 2. After the volumes were recorded each oyster was opened and its condition examined. The results of the autopsies are given in the last column. It will be observed (Column 5) that some of these apparently "healthy" oysters showed distinct injury by *Polydora* and other oysters showed a distinct abscessed condition on the gills or in the twitch muscle. All of the apparently healthy oysters produced appreciable volumes of both faeces and pseudo-faeces while those showing a distinct diseased condition, and some with doubtful appearance of health produced small or negligible deposits. Even among the healthy individuals there is a large variation in volumes and also in the ratio of $\frac{P}{F}$ as shown in Column 4. Comparison of the volumes of faeces and pseudo-faeces in the healthy oysters compared to the diseased oysters is summarized in Table 3. The healthy oysters deposited from three to five times

TABLE 2

Individual variation in feeding and rejection of suspended particles by oysters.
F, feces; P. pseudofeces

1	2				3		4	5
	First Test 48 hrs. Volume cc.		Second Test 22 hrs. Volume cc.		Sum of Volumes			
Location and No. of Oyster	F	P	F	P	F	P	$\frac{P}{F}$	Condition of the Oyster
C1, 1	1.0	8.5	1.4	7.75	2.4	16.25	6.7	Healthy
C1, 2	3.6	14.0	1.4	8.5	5.0	22.5	4.5	Healthy
C1, 3	.5	.95	.4	2.5	.9	3.45	3.8	Polydora, muscle abscess
C1, 4	.2	2.5	.2	.55	.4	3.05	7.6	Muscle abscess
C1, 5	.25	.6	.2	.60	.45	1.20	2.6	?
C1, 6	1.5	8.5	1.5	6.3	3.0	14.8	4.9	Healthy
Avg.							5.0	
C3, 1	.25	.40	.25	.40	.50	.80	1.6	Polydora, gill abscess .
C3, 2	1.60	6.4	1.0	4.40	2.60	10.80	4.1	Healthy
C3, 3	.75	3.4	.75	2.85	1.5	6.25	4.1	Healthy
C3, 4	1.2	10.7	.55	3.15	1.75	13.85	7.9	Healthy
C3, 5	.4	1.10	.30	.55	.70	1.65	2.3	Cysts in muscle, leucocytes in feces
C3, 6	.45	.90	.15	.40	.60	1.30	2.1	?
Avg.							3.7	
C5, 1	.25	1.8	.55	3.40	.80	5.20	6.5	Gill abscessed in spots
C5, 2	.70	4.4	.75	3.40	1.45	7.80	5.3	Healthy
C5, 3	.30	.70	.10	.25	.40	.95	2.3	?
C5, 4	.40	1.5	.14	.50	.54	2.00	3.7	Gill abscessed in spots
C5, 5	.75	5.0	.60	5.70	1.35	10.70	7.9	Healthy
C5, 6	.8	3.1	.80	1.65	1.60	4.75	2.9	Muscle abscessed, leucocytosis
Avg.							4.7	

TABLE 3

	Healthy (8) P	Healthy (8) F	Diseased (10) P	Diseased (10) F
Total volume produced in all compartments	102.5	19.0	23.7	6.9
Average volume produced per oyster	12.8	2.4	2.37	.69

the volume deposited by the diseased oysters under the same conditions of the experiment. These oysters were selected to show the extreme variation in the feeding behavior of a lot of oysters which externally appeared normal and free from external parasites.

The Texas-grown oysters used for most of the final experiments showed a greater uniformity in volumes of faeces and pseudo-faeces. In some experiments in which as many as 108 oysters were used simultaneously every individual produced appreciable volumes of rejecta (2 cc. to 25 cc.). However, great individual variation occurred. These facts emphasized the necessity of using (1) a sufficient number of oysters and (2) special care in selection of the animals. In the troughs shown in Figure 3, 36 oysters to the section have appeared adequate to give dependable results of general application.

The Effect of Inert Components in the Sea Water Suspension on the Volume and Composition of Food Intake, Rejecta, and the Ratio $\frac{P}{F}$

Referring to the classification of components of natural sea water suspensions (page 297) the question arises, other conditions being constant, how will the amounts of mineral particulate matter in the suspension affect the intake of the food matter by the oyster? This is the problem of the effect of the concentration of inorganic silt (from wind and wave action, or from turbid fresh water floods) on feeding by the oyster. Since we cannot readily use sporadic and naturally occurring differences in inorganic silt content in sea water, it becomes necessary to determine and maintain various but fixed ratios of concentration of inorganic to organic (food) particles in the sea water suspension. Sea water obtained directly from the pass was filtered through a cotton filter R inserted in the trap T_2 shown in Figure 3. By these means particles of the order of dimensions of diatoms were removed from the fresh sea water supply. At times when the sea water in the pass was relatively clear this filtration sufficed for all immediate experimental requirements.

In the experiment to be described a suspension of chloroplasts from the green alga Enteromorpha was used. The stock chloroplast suspension was prepared by cutting and grinding the alga in a large mortar after which it was placed in a Waring Blendor for about 10 minutes. The mixture was allowed to settle and the supernatant suspension was filtered through loose cotton to remove all particles larger than small cell fragments and the chloroplast material. This was used as a stock suspension of food which was diluted with sea water and used as a food suspension in the constant level supply jar H in Figure 3.

A dense suspension of finely ground fuller's earth was placed in jar K (Figure 3). To supply an equal and constant flow, capillary tubes of the same length and diameter as shown in Z of Figure 3, were attached to the outlets of H and K. The chloroplast suspension was delivered at the same rate to each one of Sections A, B, and C of Figure 3. The fuller's earth suspension was supplied only to Sections A and B. Thirty-six carefully selected clean "laboratory" grown oysters free from all external parasites were placed in each of Sections B and C. Section A was left without oysters.

The curves of Figure 9 show the turbidity gradients in each of Sections A, B, and C taken 26 hours after beginning of the experiment.

It will be seen that no appreciable deposition by gravity was evident in the compartments of Section A, since the turbidity was the same at inlet and outlet. The chloroplast and the finely ground fuller's earth suspension were quite stable. Hence, no corrections for deposition by gravity in Sections B and C were necessary in this particular experiment.

It is evident from curves B and C that the oysters in B did not completely clear the suspension mixture. All of the oysters in B therefore operated in a medium with a rather heavy sedimentary load. Furthermore, some of the oysters were closed part of the time. It is believed that error due to temporary closure of some of the oysters was at least in part compensated for by the relatively large number of oysters (36) used in each of Sections B and C.

At the end of 73 hours the castings and rejecta from each compartment were carefully removed, transferred to graduated centrifuge tubes, and left to settle 6 hours. The volumes of feces and pseudofeces in each compartment of sections B and C and the ratios of P/F are given in Table 4.

TABLE 4

P, pseudofeces; F, feces

Section		Compartment Number					
		1 cc.	2 cc.	3 cc.	4 cc.	5 cc.	6 cc.
B Fuller's Earth + chloroplast suspension	P	54	33	17	5	1	2.3
	F	14	8	4.8	4.0	2.5	2.5
	P/F	3.8	4.1	3.5	1.2	<1	<1
C Chloroplast suspension	P	21	7.5	4.0	0.0	1.8	0.0
	F	9	7.5	4.0	3.9	4.5	2.5
	P/F	2.3	1.0	1.0	<1	<1	<1

The table shows that adding an inert suspension to a chloroplast suspension increased the volume of rejecta and to a much less extent increased the volume of "food" intake. Comparison of the P/F ratios in Sections B and C, brings out clearly the effect of adding an inert suspension. It will be seen that as the oysters in compartments 1, 2, 3 of Section B clear the suspension the feeding behaviour of those in compartments 4, 5 and 6 of Section B return to P/F ratios similar to those in Sections 4, 5 and 6 of Section C without fuller's earth.

During the middle of the experiment at the end of 24 hours a careful check of occurrence of feces and pseudofeces was made on each of the 72 oysters. This observation showed that at this time all oysters were open and were pumping water. Eleven oysters distributed in compartments 3, 4, 5 and 6 of Section B had formed no pseudofeces. Ten of these eleven showed feces, while only one showed neither feces nor pseudofeces but was actively pumping.

In Section C only 8 out of the oysters in compartments 4, 5, and 6 showed no pseudofeces. Every one of the 36 oysters in Section C had been feeding and showed appreciable amounts of feces.

It is clear from these facts that under conditions of low turbidity and especially low concentrations or absence of fuller's earth, feeding may occur without simultaneous formation of pseudofeces.

Finally, observations have shown that pumping of sea water with a low turbidity may occur without formation of either feces or pseudofeces. Therefore it is clear that *pumping of water by the oyster is not a reliable quantitative index of feeding as has often been assumed. The only reliable quantitative measure of feeding by an oyster is the equivalent volume or weight of castings formed.* However, there is no question of the fact that inert ("non-food") components of sea water with high turbidity, decrease the rate of pumping of water by the oyster as Loosanoff and Tommers (1948) have clearly shown.

Summary

1. The capacity of an oyster to clear sea water containing a variety of types of suspended materials has been shown to be a very sensitive functional index. Its sensitivity seems to be greater than the method of measuring volume of water pumped by the oyster.

2. A method has been devised by which it is possible to measure accurately the volumes of castings and rejecta from each oyster. One hundred or more oysters may be tested simultaneously. The same procedure permits quantitative studies on rates of clearance and feeding of substances under controlled conditions, an accurate approach to many problems of oyster physiology.

3. Quantitative measurement of the castings is a reliable equivalent measure of the feeding process of an oyster. Water propulsion is not a reliable quantitative measure of feeding.

4. The ratio $\left(\frac{\text{Volume of rejecta}}{\text{Volume of castings}}\right)$ is a valuable functional index for studies on the oyster.

5. As the sedimentary load in the sea water medium of an oyster increases, the ratio $\frac{\text{Volume of rejecta}}{\text{Volume of castings}}$ increases.

6. Oysters in sea water of very low turbidities may form castings without rejecta. In rare cases it appears that feeding may stop but rejection continue. In sea water of very low turbidity, it was observed in a few cases that pumping occurred without formation of castings or rejecta.

7. In sea water of low turbidity, increase in velocity of flow compensates for low concentration of suspension, so that where other factors are the same, the volume of food intake increases with increased velocity of flow. Practical application of this principle is discussed.

8. Oysters of the same size and age and free from external parasites may show marked differences in feeding behaviour. Sick or abscessed oysters do not feed normally.

9. The quantity of inert matter (fuller's earth) in a suspension of both chloroplasts ("food") and fuller's earth in sea water determines in part the relative and absolute volumes of food intake and the volumes of rejecta in the same oyster.

10. There appears to be no reason why the above facts derived from laboratory observation may not be applied to relations of the oyster to turbidity under field conditions.

LITERATURE CITED

Damas, D. 1935. Le role des organismes dans la formation des vases marines. Ann. Soc. Geol. Belg., 58: 143.

Fox, D. L., H. V. Sverdrup, and J. P. Cunningham. 1937. The rate of water propulsion by the California mussel. Biol. Bull., 72: 417–438.

Grave, C. 1901. The oyster reefs of North Carolina. Johns Hopkins Univ. Circ., 20: 50–53.

————. 1905. Investigations for the promotion of the oyster industry of North Carolina. Report U.S. Fish Comm., 1903, 29: 247–315.

————. 1916. The process of feeding in the oyster. Science, 44: 178–181.

Kellogg, J. L. 1915. Ciliary mechanisms of Lamellibranchs, with descriptions of anatomy. Jour. Morph., 26: 625–701.

Loosanoff, V. L. 1949. On the food selectivity of oysters. Science, 110: 122.

————, and J. B. Engle. 1947. Effect of different concentrations of micro-organisms on the feeding of oysters. Fishery Bull., 42, Bull. U.S. Fish and Wildlife Serv., 51: 31–57.

————, and F. D. Tommers. 1948. Effect of suspended silt and other substances on rate of feeding of oysters. Science, 107: 69–70.

Lotsy, J. P. 1893. The food of the oyster, clam, and ribbed mussel. Rept. U.S. Comm. Fish and Fisheries, 19: 375–386.

Nelson, T. C. 1923. The mechanism of feeding in the oyster. Proc. Soc. Exp. Biol. Med. 21: 166–168.

Yonge, C. M. 1926. Structure and physiology of the organs of feeding and digestion in *Ostrea edulis.* J. Mar. Biol. Assn. U.K., 14: 295–386.

ZoBell, C. E., and W. A. Landon. 1937. Bacterial nutrition of the California mussel. Proc. Soc. Exp. Biol. and Med., 36: 607–609.

Self-Silting, Survival of the Oyster as a Closed System, and Reducing Tendencies of the Environment of the Oyster[1]

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In the preceding paper it was shown that the turbidity and self-silting by the oyster may be important factors in developing and determining the nature of the environment of the oyster.

The practical importance of self-silting appears to be inversely related to the velocity of flow of the sea water medium at the surface of the oyster bed. In order to prevent the effects of self-silting this velocity of the water surface of the bed must be maintained sufficiently high to remove the continuously accumulating self-silt deposit as well as that part of the silt deposit which is caused by gravity. The relative amounts of self-silt and silt by gravity and their total quantity determine the magnitude and effectiveness of the required maintained velocity of flow for preventing the oyster from ultimately becoming buried.

Besides endangering the oyster by ultimately reducing its food supply and its feeding capacity, self-silting with minimal silting by gravity results in a reduction of availability of oxygen for an aerobic type of respiration.

To indicate in a quantitative manner how the oyster may be related to consequences of self-silting we shall use two convenient indices, namely, (a) the survival time of the oyster as a closed system under conditions of maintained shell closure and (b) the development, distribution and magnitude of the reducing tendency—so-called red-ox potential—of the oyster's environment.

Survival Capacity of the Oyster as Shown by Maintained Closure of the Shell

In closing its shell the oyster at once not only imposes upon itself an anaerobic existence but also a change in life processes from conditions in an open to those in a closed system. The capacity of the oyster to survive complete closure of the shell should be a useful general physiological index for various studies on the metabolism of the oyster.

It is common knowledge that the oyster can survive periods of complete closure, especially at lower temperatures. However, no quantitative data are available which would give any adequate information about the length of survival time. The following experiment was performed.

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[1] This investigation was supported by funds from the Texas A & M Research Foundation. Editor's note: This manuscript was submitted in 1950 as part of project 9 of the Texas A & M Research Foundation on work carried out at the Institute of Marine Science at Port Aransas and is published in essentially original form.

Survival After Closure During Winter Season

The experiment to be reported involved the use of 880 oysters. These oysters came in two carefully selected lots of 443 and 437 each from Long Reef in Aransas Bay, and from Copano Bay. After being removed from the reefs and carefully culled for uniform size, the oysters were left for five days in large laboratory tanks with large volume flow of sea water to permit adjustment to salinity and allow for initial mortality due to culling.

Two hundred forty-one oysters from Copano Bay were closed tightly under water by means of heavy rubber bands. Similarly, 232 oysters from Long Reef were closed. One hundred ninety-six oysters from Copano Bay and 210 oysters from Long Reef were left open as controls (Table 1).

TABLE I

Duration of Anaerobic Period, hours	145	170	218	270	312	336	384	432	
Sample Number	1	2	3	4	5	6	7	8	
COPANO BAY									
Number of oysters used in the sample	39	39	39	13	13	30	30	38	Total=241
Number of surviving oysters	17	28	10	2	2	0	1	0	
Per Cent Survival	44	72	25	15	15	0	3	0	
LONG REEF									
Number of oysters used in the sample	38	39	39	13	13	30	29	31	Total=232
Number of surviving oysters	26	28	23	5	5	1	2	0	
Per Cent Survival	68	72	59	38	38	3	7	0	

Controls: Copano Bay—open oysters—194 out of 196 oysters living at end of 432 hours.
Long Reef—open oysters—158 out of 277 oysters living at end of 432 hours.

All the oysters from each of the two localities were placed in large tanks with equal volume of water flow. The salinities varied from 17.8‰ to 13.2‰ and the temperature from 23° C. to 14° C. during the experiment which lasted 18 days, from November 12 to November 30, 1947. The salinities and temperatures in the tanks and the pass were both respectively nearly the same.

In order to determine how long the closed oysters could survive anaerobically (more precisely as closed systems), samples from each lot of Copano Bay and Long Reef oysters were taken at the end of different periods of exposure to closed conditions. The rubber bands were removed under water. Mortality and the number of live oysters were carefully determined in each of these samples. The remaining living oysters of each sample were replaced in the running sea water in the tank and carefully watched for subsequent mortality or recovery after unbanding. The results indicated that the prolonged closures had produced irreversible injury depending upon duration of closure.

Table 1 shows the per cent of survival in the samples of oysters *immediately* after unbanding. The separate results for both Copano Bay and Long Reef oysters are similar; however they show that there are very great differences in survival time of individuals under closure conditions in these reef grown oysters. This great range of variability is undoubtedly of great significance for purposes of further physiological and biochemical analysis of its causes. This problem must be left for the future.

The oysters which survived closure showed a high mortality after being returned to open and aerobic conditions. The total number of such oysters from all the samples which were alive at the end of the 432-hour period of the experiment were 7 oysters from Copano Bay and 39 oysters from Long Reef, or 46 oysters out of a total of 473 oysters. The number of oysters of samples 1, 2, 3, 4, 5, 6, 7, and 8 which survived the closure periods of 145, 170, 218, 270, 312, 336, 384, and 432 hours and also survived to the end of the 432-hour period, were respectively in the Copano Bay lot: 2, 1, 4, 0, 0, 0, 0, 0, and in the Long Reef lot: 19, 12, 8, 0, 0, 0, 0, 0. These high mortality results indicate that there is difficulty in adjustment after a sudden return to an aerobic environment. As might be expected, this readjustment of the oyster to an aerobic medium become more difficult as the duration of the anaerobic period increases.

The facts brought out in the experiment are of practical importance. Little mortality occurred in the 406 control oysters except during the beginning period of 145 hours when 33 oysters died of the Long Reef lot. This somewhat unusual result remains unexplained. However, the general results of the experiment are very clear.

Survival After Closure During Summer Season

A second experiment was performed during the first week in August of 1948. The temperature during this experiment varied from 26.8° C. to 31.4° C. in the large experimental tanks. Salinities varied from 35.82‰ to 36.64‰.

Two hundred one 3½″ oysters, and 109, 1½″ spat were closed with rubber bands. One hundred oysters, and 50 spat were left open as controls. The procedure of this experiment was similar to the one described in detail above and, therefore, details will be omitted.

The final results may be summarized by saying that all of the 3½″ closed oysters were dead at the end of 171 hours. A few spat (1½″) lived to a maximum of 195 hours duration of closure of the shell. Only 12 oysters of the 100 controls were dead at the end of 195 hours. Forty-seven spat out of the 50 used as control were alive at the end of 195 hours.

Although the oysters used in this experiment were of necessity not comparable in history with those used in the first experiment it was clearly evident that the survival capacity of these oysters at approximately 15° C. higher temperature was only about one-half, or less, of the survival capacity in those tested during the winter months in the first experiment.

The Possible Significance of Distribution of So-called Redox Potential in the Environment of the Oyster

Much has been written about the so-called redox potential in complex biological systems, such as bacterial cultures, soils, etc. As a result the concept of the redox potential, which has a very specific meaning and definition in the physical chemistry of simple systems, has come to be clouded and used in a careless manner in much experimental work in biology.

In the present paper the difference in potential observed between a saturated calomel half cell and a platinum wire immersed in the same system will merely serve as an approximate index of the *reducing tendency* of the medium in which the platinum surface is immersed, without making any attempt at identifying quantitatively the electromotively active ion species of the complex system which determine the potential of the platinum electrode.

When used with precaution in this very general sense, the observed but somewhat unstable potential of the platinum electrode affords a fairly useful approximate index of the general reducing and oxidizing tendencies of a biological system.

Since, when self-silting by the oyster occurs, a large fraction of the self-silt is organic in origin, the silt layer becomes a depository of relatively large amounts of free energy available to micro-organisms. Therefore, the self-silt layer around the oyster would be expected to be the site of bacterial decomposition accompanied by high rates of oxygen consumption and consequent tendencies toward a strongly reducing anaerobic environment. In castings from the oysters in the experimental trough the black FeS formed within four days even in the presence of a stream of aerated sea water.

The measurement of the vertical distribution of this reducing tendency by means of the platinum electrode becomes a useful approximate criterion of the "respiratory environment" of the oyster.

For the purpose of obtaining specific information based on laboratory experiments the following aquaria were set up. Glass cylinders, 150 mm. in diameter by 300 mm. high were filled to a height of 50 mm. with a layer of fine washed beach sand.

Each cylinder was supplied with running sea water, the velocity of flow of which was regulated to equal volume by pinch cocks on rubber siphons from the same constant level supply tank.

In one typical experiment the results of which are given in Figure 1, curves A, B, and C, three identical cylinders were used. All were filled with a 50 mm. layer of washed sand and supplied with a constant stream of sea water as shown in Figure 1.

One cylinder A (curve A), was left without oysters. To B (curve B) was added one oyster, while five oysters were placed in C (curve C). The position of the oysters is indicated in the diagram drawn to scale in Figure 1. At the end of eight days a silt layer about 5 mm. thick had formed by gravity in the blank cylinder A. The oysters in B and C had in addition deposited a considerable quantity of self-silt.

At the end of eight days all oysters were open and alive.

The potential in millivolts of a platinum electrode against a saturated calomel half cell was determined at different positions (ordinates, Figure 1) in a vertical direction beginning at the surface of the sea water and ending at the bottom of the sand layer.

The vertical distribution of the observed potentials are shown by the graphs A, B, and C in Figure 1. It will be seen that the potentials in the sea water layer in A were the same from the air surface to the upper surface of the silt layer. As the electrode surface (about 1 sq. mm.) entered this silt layer, wihch was brownish in color and contained considerable numbers of diatoms, the potential became more positive, evidently due in part to a slightly higher concentration of free oxygen produced by the diatoms. As soon as the electrode entered the sand layer the potential became rapidly negative to a maximum of about 150 millevolts. This is the usual type of curve obtained in such blanks.

The same kind of measurement was made in cylinders B and C containing oysters. These are shown in curves B and C. The position of the upper surface of the silt layer in each aquarium at the point where the electrode entered the surface is indicated by the horizontal line T on each graph. The important fact to note about graphs B and C is that the potential in the silt and sand layer has become very highly negative, in fact a part of the self-silt layer and the sand in C has become even electro-negative to the hydrogen electrode which means that the reducing tendencies of the medium are so great that other conditions being standard, free hydrogen would be given off to a normal hydrogen electrode.

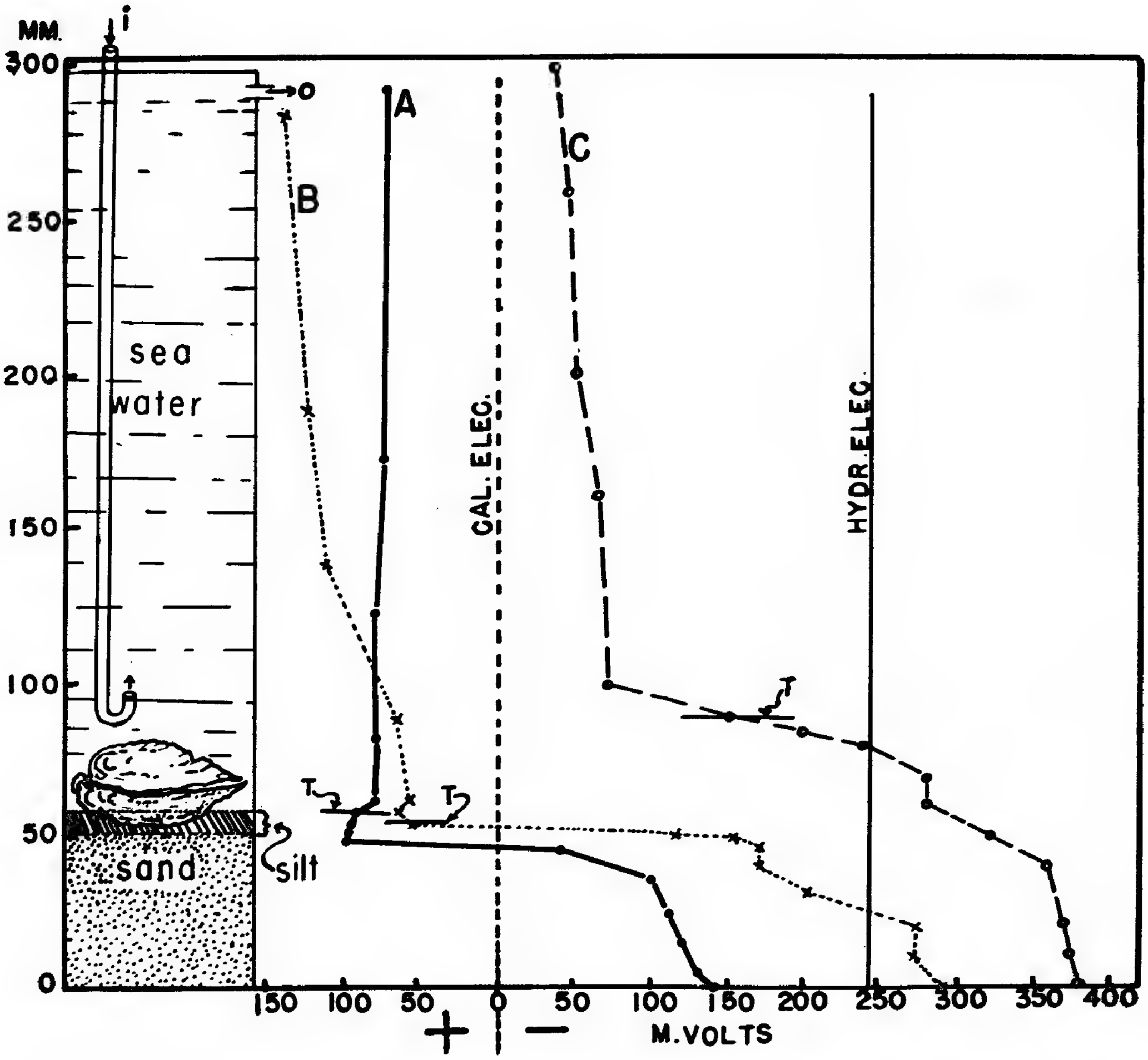

Fig. 1.

It is manifestly under such reducing conditions in the levels between say 50 mm. and 100 mm. in the aquarium C, that the anaerobic capacity described above in the survival experiments under forced shell closure, comes into play. The oyster in this position is of necessity called upon to survive in a semi or wholly anaerohic environment, even though it operates as an open system.

It is obvious that if the oyster under such conditions cannot depend upon removal of the self-silt layer by a water current of *adequate* velocity, then its margin of anaerobic safety may very soon be exceeded even though this margin under closure, as shown above in Table 1, be several days.

The possible significance of self-silting for the oyster, with a relatively high content of organic matter in the self-silt, should now be clear.

In such aquaria if an accumulation of self-silt is permitted even with a strong flow of sea water, the oysters soon die, with prompt simultaneous development of a very characteristic "black layer" (Fe S) in the sand. See Bruce (1928.)

Repetition of the above type of experiment gave the same general types of curves. The self-silting always produces a marked shifting of the curves to the right, some potentials reaching the low negative value of 600 millivolts.

If now, as shown by the experiments on anaerobic survival, the temperature is raised from 15° C. to 30° C. as generally occurs in Louisiana and Texas bays during the summer season, then the rate of development of the self-silting and accompanying anaerobic environment would be expected to reduce the survival time of oysters in such environments.

It must be observed that different oyster individuals on a natural bed are subjected to different degrees of such anaerobic self-silting hazard and, therefore, it might be expected that on most oyster beds which are not continuously desilted by water currents some oysters in unfavorable positions on the reef would practically always be subject to mortality, with consequent adjacent *subsurface* self-pollution and development of the black layer. This is probably the reason that the black layer with high hydrogen sulfide content so frequently occurs under many oyster beds.

The Increase in Reducing Tendency of the Mantle Chamber Fluid During Shell Closure

A very fine insulated platinum wire with an exposed clean metal surface at the tip was inserted through a small notched opening between the valves of an active oyster. The oyster was then stimulated to close its shell. When closed a clamp was quickly placed on the valves to keep them closed. Measurements show that the potential of the sea water fluid in the mantle cavity steadily decreases until a negative potential of 250 to 300 millevolts is reached indicating that the immediate environment of the oyster tissues becomes strongly reducing under anaerobic conditions. Probably this drop in potential is largely due to decrease in dissolved oxygen, since the mantle fluid is strongly buffered by calcium dissolved from the shell under condition of shell closure in the same manner as was shown to occur in *Anodonta cygnea,* by Dotterweich and Elszner (1935) and others.

Summary

1. When oysters are placed as a closed system under anaerobic conditions by forced closure of the shell there is a wide range of survival capacity as measured by survival time of different oysters. The survival time varied from about two days to sixteen days during the low winter temperature range of 14° C. to 23° C. In a less extensive experiment carried on during the summer season with a temperature range between 26° C. and 31° C., maximum survival time under closure conditions of the oysters was about 7 days. What determines these great differences in survival time—as a closed metabolic system in different individual oysters—remains a fascinating problem for the future.

2. It is to be expected that the capacity of any oyster to survive anaerobic conditions for a considerable period of time serves as a protection against the hazards often imposed by sedimentation and self-silting.

3. Self-silting which involves in part deposition of large quantities of organic matter leads readily toward the establishment of semi or highly anaerobic conditions around the oysters. Oysters therefore normally require a sufficiently rapid flow of water to prevent continued self-silting. Self-silting if not prevented would become a self imposed hazard often of much greater importance than silting by gravity under the same conditions.

4. The reducing tendency as measured by the platinum electrode is a useful index of the anaerobic conditions of life in the environment of the oyster.

5. It is common practice by oyster growers to transport oysters under conditions of forced closure from one locality to another. If such closure occurs at high summer temperatures of 30° C.–35° C. as may often happen, then in general a considerable mortality may be expected if such closure lasts for more than 24 hours, since the anaerobic capacity and survival under closure of some oysters in a population is quite limited.

LITERATURE CITED

Dotterweich, H., and Elszner, E. 1935. Die Mobilisierung des Schalenkalkes für die Reaktionsregulation der Muscheln (*Anodonta cygnea*). Biol. Zentralbl., 55: 138–163.

Bruce, J. R. 1928. Physical factors on the sandy beach. Part II. Chemical changes—carbon dioxide concentration and sulphides. Jour. Mar. Biol. Assn. U.K., 15: 553–565.

Self-silting by the Oyster and its Significance for Sedimentation Geology[1]

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Every investigator who has studied the oyster is familiar with the fact that when oysters are kept alive in running sea water aquaria in the laboratory the oysters sooner or later become partially or wholly covered with a layer of sediment. This is illustrated in Figure 1, A and B. Figure 1 B shows the extent of deposition over nine carefully cleaned healthy oysters placed in an aquarium through which sea water from Aransas Pass was allowed to flow continuously at a rate of about two liters per minute for six weeks. Figure 1 A shows the condition at the beginning of the experiment. The turbidity as measured in the Fischer turbidimeter varied from 60% to 95% transparency using the transparency of distilled water as 100%. Coarse sedimentary particles were caught in the flask used as a trap.

The time required to accumulate such a layer of sediment would to the casual observer obviously depend upon (1) the sedimentary load *i.e.* grams of suspended solids per liter of sea water, (2) the density and size of the suspended particles, (3) the velocity and degree of turbulence of the water stream through the aquarium, and (4) the concentration of ions *i.e.* the salinity of the sea water. Lastly, (5) the rate of deposition would also depend on the production of castings and rejecta produced by the oyster in the process we shall call self-silting.

The purpose of the present paper is to present some quantitative data which show the relative importance of gravity and self-silting by the oyster in the deposition of the sedimentary layer in laboratory experiments and to raise the question of the possible applications of these facts to certain types of oyster beds in the field.

It must be understood at the outset that before the facts from the laboratory observations can be considered definitely applicable to field conditions, it is of paramount importance that suitable field observations be made.

The author also believes that some of the following facts may be of interest to the student of sedimentary geology.

Comparison of Sedimentary Volumes Deposited By Gravity And By the Oyster

The following laboratory experiment was performed. Three identical aquaria each 23 x 11 x 10½ inches high were arranged to receive equal and constant supplies of sea water from a fourth aquarium arranged to give a constant and equal head of hydrostatic pressure to each one of the three experimental aquaria.

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[1] Editor's note: This manuscript was submitted in 1950 as part of Project 9 of the Texas A & M Research Foundation on work carried out at the Institute of Marine Science at Port Aransas. Suggestions by W. Armstrong Price are gratefully acknowledged.

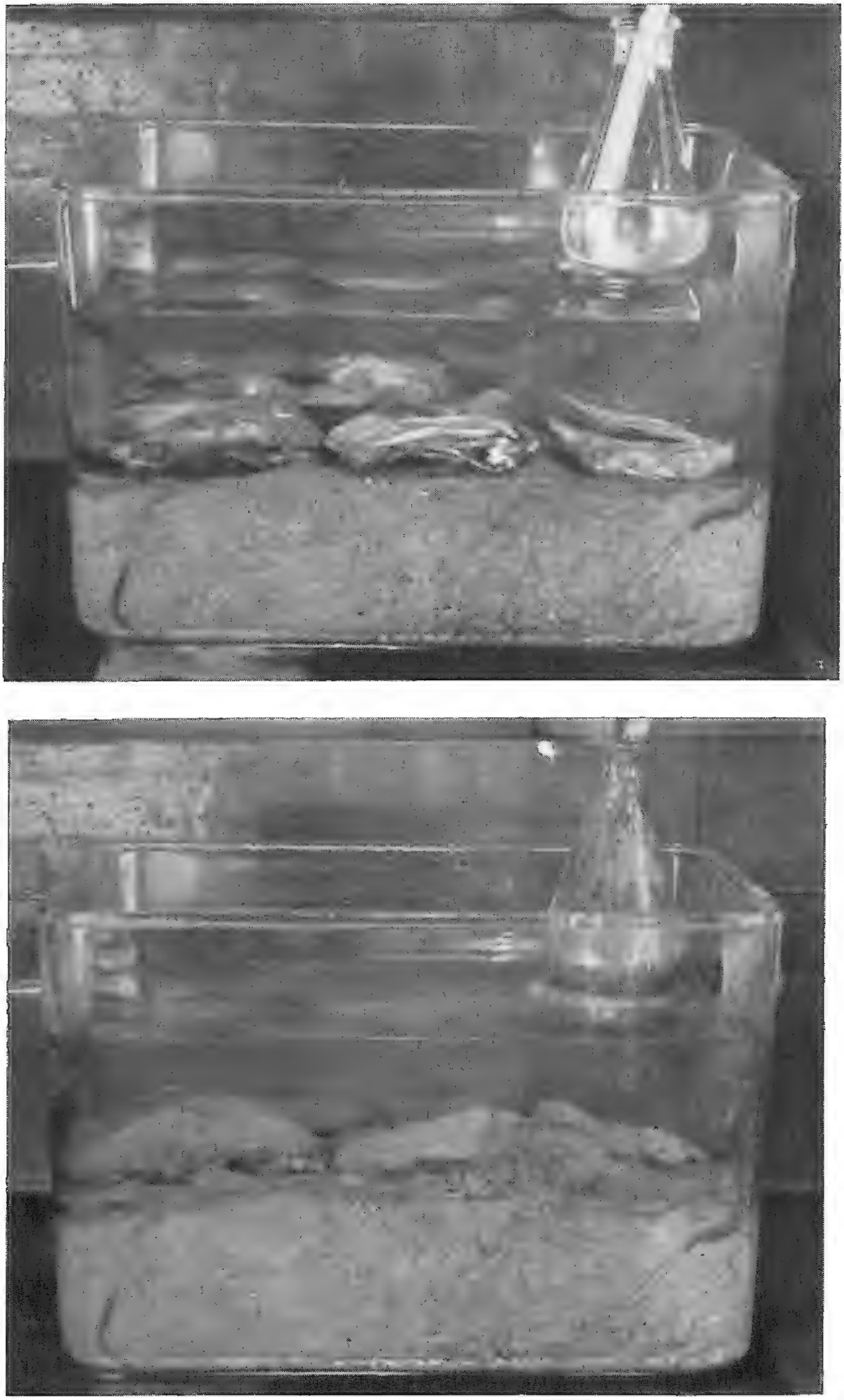

Fig. 1. Oysters in Aquarium in self silting experiment. A. At Start; B. After 12 days.

The volume flow of sea water to each aquarium was adjusted and maintained at 1930 cc. per minute, or 115.8 liters per hour. The depth of water layer in each of the three aquaria was 12 cm. and was maintained constant.

Thus the volume of sea water in each tank was 19.15 liters and therefore each aquarium received a complete change of sea water six times per hour.

The flow through the aquarium was provided without turbulence by allowing the sea water to enter and overflow a wide mouth 1000 cc. Erlenmeyer flask placed on the bottom of the aquarium. This flask, together with the overhead constant-level supply tank, served as sediment traps for any heavy particles.

Twenty actively growing oysters 2 to 2.5 inches long were placed and regularly spaced on the bottom of aquarium C. Twenty empty oyster shell boxes, closed with a rubber band, were placed on the bottom of A, and aquarium B was left blank without oysters or shells. Since the total sedimentary deposit by gravity will depend upon the surface area of "bottom" for deposition, the shell surface in aquarium A was provided to approximately equal the shell surface in C upon which passive deposition by gravity occurred in addition to the exposed bottom area of the aquarium.

The experiment was continued for 12 days, 288 hours.

The turbidity was determined once each day, using the Fisher electrophotometer and considering transmission of distilled water 100%. The daily turbidities of the sea water taken from the outlet of each aquarium are shown in the correspondingly labeled curves A, B, and C, Figure 2.

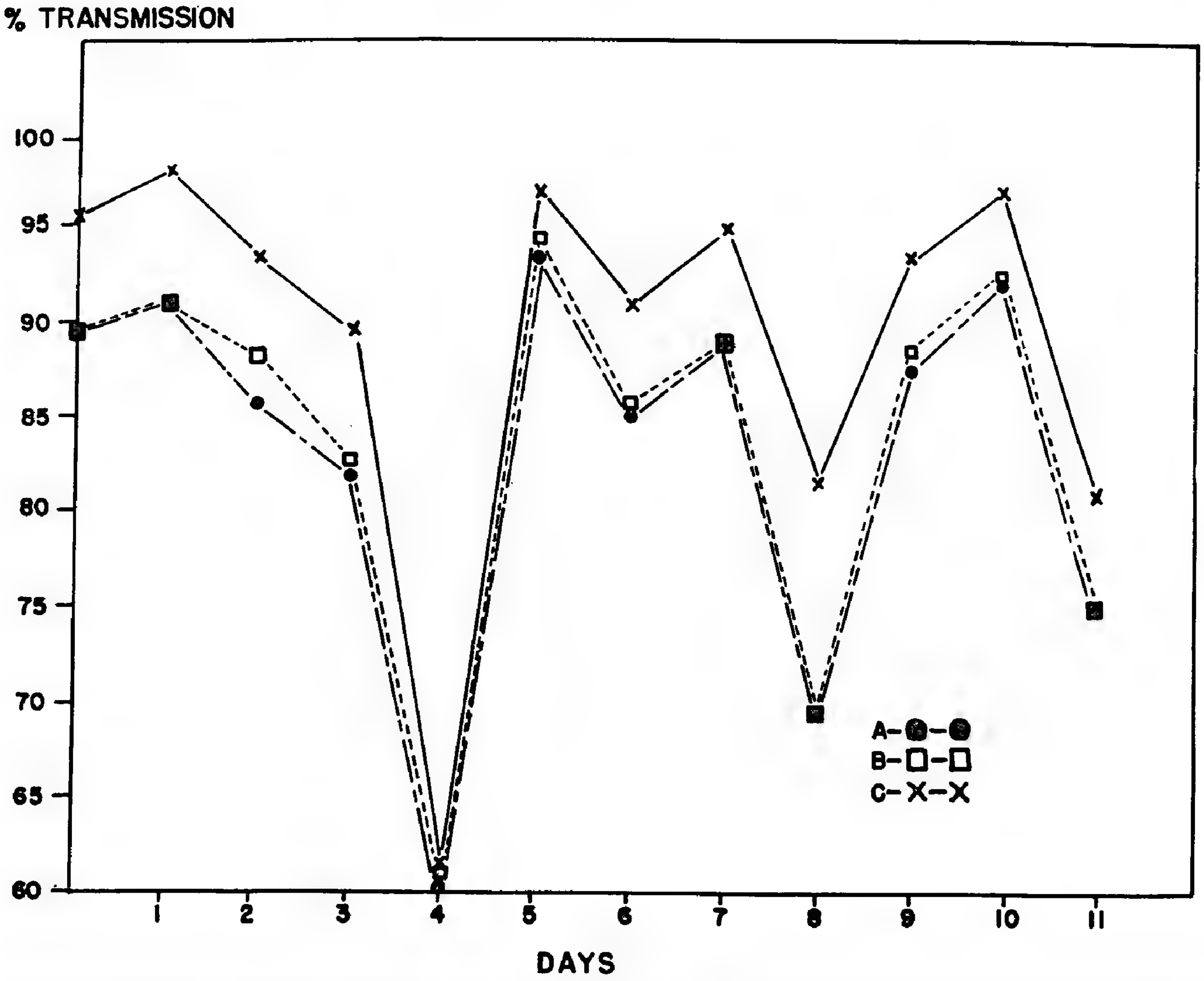

FIG. 2. Turbidity of the water flowing out from aquaria. A, with empty oyster shells; B, empty aquarium; C, with live oysters.

It will be observed, (1) that the oysters in C always caused some clearance of the sea water, (2) that gravity caused only a very small amount of clearance in B with empty shells over that in A without shells. This difference was often within the limits of error in measurement. (3) The transparency of the sea water supply was very high with the exception of a short period during the fourth, eighth and eleventh days. At times during the experiment the sand bottom by the laboratory dock at a depth of six feet was clearly visible. Salinity of the Pass at Port Aransas throughout the experiment varied between 26‰ and 28‰. The temperature of the sea water in the aquaria was 21° C. and varied only within a few tenths of a degree from that in the Pass. All oysters in C were living and active at the end of the experiment.

At the end of 288 hours the oysters and oyster shell boxes in C and A were carefully cleaned and all sediment on the bottom of each aquarium was collected in 1000 cc. graduated cylinders. Similarly the sediment caught in the 1000 cc. flasks used as overflow traps, was placed in 100 cc. cylinders. After 5 hours settling of the sediment in the cylinders the photograph in Figure 3 was taken.

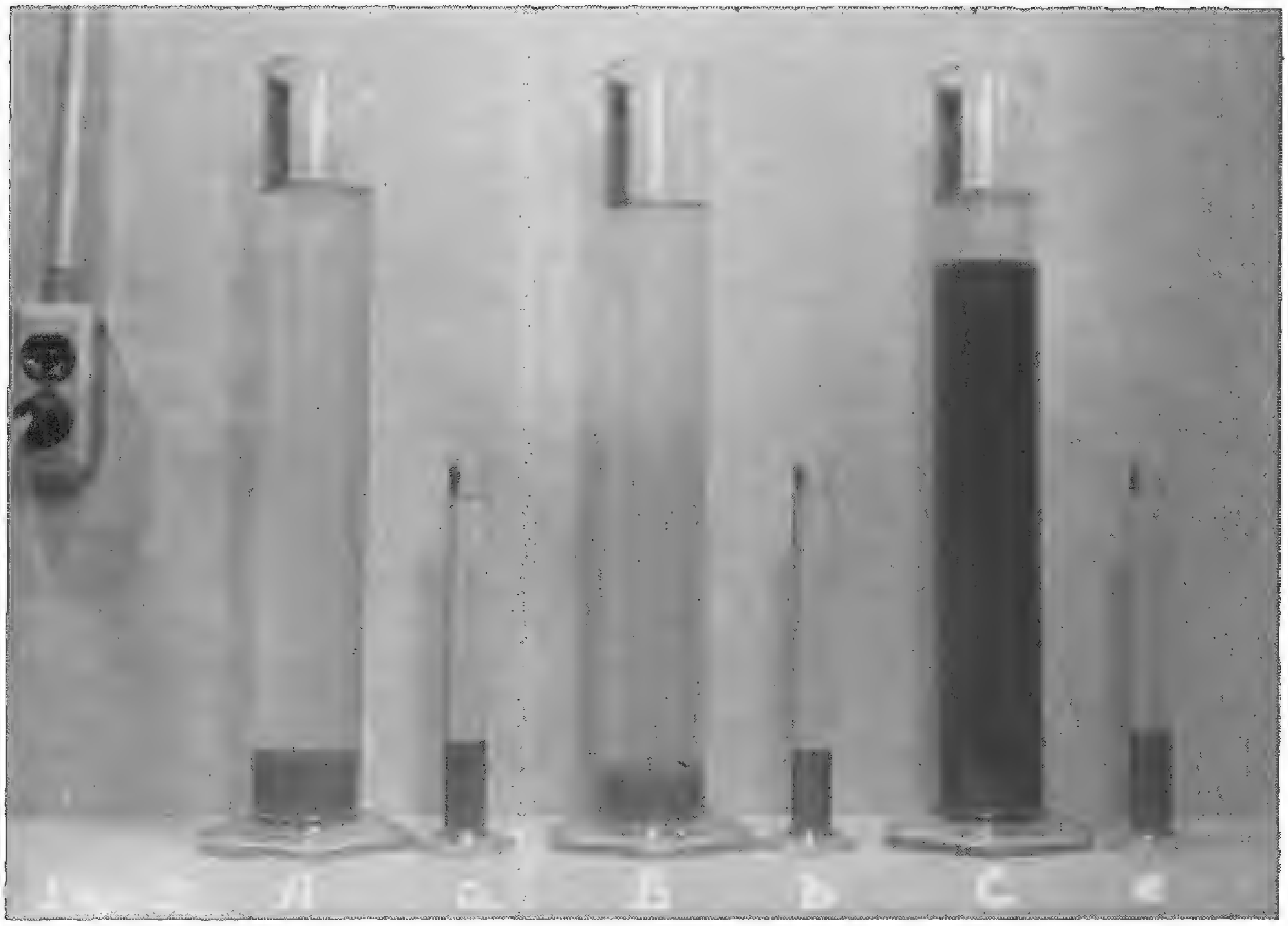

FIG. 3. Sediment from self-silting experiments after 5 hours settling. Sediment from aquaria in large cylinders; sediment from overflow traps in small cylinders. Aquarium A, with empty shells; B, empty; C, with live oysters.

After about ten hours of settling when the volumes in the cylinders approached an approximate minimum, the volumes of sediment were as follows: A=85 cc. B=60 cc. and C=755 cc. The dry weights of A and C were 31.3 gms. and 197.2 gms., respectively. B was lost.

If the volume of deposit in C is corrected for by subtracting from it the volume of deposit in A, caused by gravity, then the experiment shows that the 20 oysters deposited

7.88 times the volume of sediment deposited by gravity under the same conditions on the same bottom area. In dry weight the oysters deposited 5.3 times the amount deposited by gravity alone. Calculations based on the average diameter of these 20 oysters show that they covered approximately ½ of the area of the bottom of the aquarium.

The observed volume of 670 cc. deposited on 253 sq. inches equals 40.9 cu. inches. At this rate of deposition by a similar layer of oysters under these same conditions, there would be deposited by self-silting alone, on one acre a volume equal to 24.88 cubic yards in twelve days. Since the layer of oysters covers only approximately one-half of the area, the thickness of the silt layer which would be deposited during twelve days on one acre, would be approximately 0.33 inch. The average thickness of the oysters used in the experiment was somewhat less than one inch, therefore, at the observed rate of deposition it would only require approximately 36 days to deposit one inch of silt, or enough on the average, to barely cover this layer of oysters.

Now the first fact to remember is that the silt load in the sea water used in this experiment was very *low* as shown by the general high transparency, in curves of Figure 2. Second, it has already been shown in the previous experiments, see photograph Figure 7 and curves of Figure 8 in Lund (1957), that the total self-silt deposit by the oyster is increased exponentially as the turbidity is increased. The rate of this self-silting at a light transmission of 70–80% is from three to five times the rate of self-silting at turbidities corresponding to transmission of 90–95%. This fact means that the rate of observed deposition by the oysters in the above experiment was of a comparatively small order of magnitude. With high turbidities the expected rate of deposition would be approximately 3–4 times the observed value or at a rate which would have deposited by self-silting alone the observed amount of silt in 3 to 4 days instead of twelve days and the oysters would have been covered in 9 to 12 days, *not* by gravity but by their own self-silting process under conditions of the laboratory experiment.

The volumes deposited by 38 oysters in each of the two aquaria in this experiment during eleven days were 970 cc., and 1000 cc., respectively. Subtracting the controls which had corresponding deposits of 140 cc. and 165 cc. we obtain 830 cc. and 835 cc. of self-silt deposited by each of the respective lots of 38 oysters. The area of the bottom of each one of the aquaria in this experiment was 345 sq. inches upon which was deposited an average of 832 cc., or 50.8 cu. inches, of oyster silt in eleven days. This is equal to 19.8 cu. yards of silt deposited on one acre by a layer of oysters covering 190/345 of an acre. If the single layer of these oysters were crowded so as to cover all of the area of one acre then the volume of oyster silt which would be deposited on one acre in eleven days would equal 35.9 cu. yards. The equivalent dry weight would be 8.36 tons deposited by a uniform single layer of oysters in 11 days.

The results of these two independent experiments correspond well with one another.

Five additional experiments of shorter duration were performed using only three oysters in a rectangular glass dish through which was flowing a constant stream of sea water at accurately known rate. Two additional dishes were set up. Dish A contained no oysters. Dish B contained three oyster shell boxes, closed with rubber bands. A and B served as controls for C as usual. All three dishes in each experiment received the same rate of flow. The results of the five experiments of different lots of three oysters each are given in Table 1.

The sedimentary load in cc. per liter was determined by centrifuging 500 cc. or 1000 cc. samples taken from the inlets to the dishes A, B, C. The average sedimentary load is

TABLE 1

1	2	3	4	5	6	7				8	9
						Total Volume Deposited					
Exp.	Duration Hours	Flow Rate Lit./Hr.	Total Volume Flow Liters	Average Sedimentary Load cc./Lit.	Total Sed. Load cc.	A cc.	B cc.	C cc.	Oyster C-B	Per Cent Efficiency of Oyster C-B / Tot. Sed. Load x 100	Ratio C-B / B
1	89	17.7	1,575	......	......	20	24	168	144	......	6.0
2	48	32.9	1,579	0.32	505	12	14.6	131.5	116.9	23.1	8.3
3	72	32.5	2,340	0.18	421	10.2	12.2	64	51.8	12.4	4.3
4	46	32.5	1,495	0.14	209	4.5	6.2	17	10.8	5.1	1.7
5	48	31.5	1,512	0.19	287	6.0	8.0	40	32.0	11.1	4.0

given in column 5 of the table. The total load carried by the total volume of sea water column 4 which flowed through each dish during the experiment is given in column 6. Column 7 is self-explanatory and together with the data in column 6 yields what in column 8, under the particular conditions, we shall call the "efficiency" of the oyster as a depositor of self-silt from the average sedimentary load.

In these experiments the efficiency of the oyster as a depositor of self-silt varied from 5.1% to 23.1% of the total sedimentary load which passed over the oysters during the experiment. The data in column 9 agrees in general with the result obtained in previous experiments, and shows that as the sedimentary load (equivalent to turbidity) diminishes, the self-silt deposit decreases, see column 7, C–B. Similarly, the relative "efficiency" of removal of suspended particles diminishes with decrease in concentration of the suspension. This is the same result which was obtained by a different but more accurate procedure in the experiment reported previously by Lund (1957).

Laboratory experiments clearly indicate that as self-silting reaches a point where the size of the opening of the oyster to the sea water becomes limited by the silt layer—see Figure 1—the rate of self-silting diminishes and, therefore, in all probability the capacity of the oyster to feed because of the restricted access to the water over the bed. The experiments indicate, however, Lund (1957), that if the concentration of food near the bottom is high the oyster might obtain an adequate food supply even for fattening. However, as the self-silting increases, the margin of safety for the oyster becomes inevitably more limited and the hazards increase under conditions of the laboratory experiment.

There are, of course, two ways in which the effects of self-silting may be allayed or compensated for in the field, namely, (1) by water currents caused by tides and wind, and (2) the usual self cleansing action of the oyster when the valves are suddenly closed.

However, if it should happen that the oyster bed experiences relatively quiet water, where current movement is at times inadequate to move the sediment due to self-silting, then the oyster would be left practically with only the one remaining means of cleansing, namely, shell closure. Every observer of oyster behaviour has seen both in the laboratory and in certain favorable field locations that oysters often are nearly covered by self-silt, but lie in a partial depression in the self-silt layer, with a small opening exposed to the free water which is kept open by repeated closure of the shell. The practical question regarding the effect of self-silting is: just what does happen on an area where oysters are planted or on an oyster bed which occupies a location where the water currents are at certain times inadequate for removal of the self-silt deposit? This question which is posed by the above laboratory experiments can only be answered by carefully planned and executed observations on, for example, a specially selected location of an oyster bed. It seems obvious that in an actively-growing oyster reef, water currents must be adequate for removal of all silt.

Observations show that the self-silt deposit by the oyster is flocculated or somewhat coherent and resists displacement by flow traction much more than the same silt components precipitated by gravity, therefore the cleaning of an oyster bed by traction would demand a faster flow of water than that required for movement of the same components deposited by gravity. Furthermore, even if the oyster bed is cleaned by tidal currents or wind action the material of the self-silt deposit does not readily return (deflocculate) to its original finely divided state as shown by shaking the self-silt deposit with sea water. It is clear from these facts that the oyster facilitates deposition of suspended sediments whether or not the oyster bed is cleansed by water currents.

Finally, attention is called to the fact that many associated animals, such as the tube-dwelling crustacea and annelids, greatly augment the deposit by their own self-silting process so that the results of the laboratory experiments are *minimum* rather than maximum values.

Importance of Self-silting for Sedimentary Geology

On the basis of the above experiments it will be evident that oysters by means of self-silting even in waters of relatively low turbidity, are agents many times more effective than the ordinary process of sedimentation by gravity on the same area. If we note the fact that the percentage of inorganic material in the dried self-silt of the oyster is about 73%, then it is evident that out of the calculated 35.9 cu. yards which according to our experiments would be deposited on one acre, by one layer of oysters alone, would be 26.2 cubic yards—or 6 tons of dry mineral matter.

Summary

1. Laboratory experiments showed that normal oysters under laboratory conditions, deposited by self-silting approximately eight times the volume of sediment deposited by gravity alone under exactly the same conditions of sedimentary load, velocity and volume flow of sea water and bottom area of deposition. This confirms the results from previous experiments in which six to twelve times the volume of silt deposited by gravity alone was deposited by the oyster.
2. The experiments show that at relatively low turbidities ranging from 70% to 95% light transmission a single layer of oysters covering one-half the bottom area can produce sufficient silt deposit to completely cover themselves in thirty-six days, if the self-silt deposit is not removed by external forces.
3. Calculations on the basis of the experiments show that the volume of self-silt produced by a single continuous layer of oysters in eleven days, on an area of one acre would amount in volume to 35.9 cubic yards. The equivalent dry weight would be 8.36 tons.
4. Definite relations exist between volume of self-silt deposit, sedimentary load, and volume flow.
5. It has been shown that self-silting may increase the hazards under which the oyster lives. This applies to food supply, aerobic respiration and may apply to other environmental factors.

6. On the natural oyster bed the self-silt deposited by the oyster is very often augmented by self-silt produced by other commensal organisms attached to oysters.

7. The practical importance of self-silting for the life of the oyster depends upon whether or not external forces, due to wind, waves, and water currents are *sufficiently* strong to maintain a removal of the self-silt deposit. Thus the practical importance of self-silting is only significant in oyster habitats where the velocity of *bottom* currents are inadequate. It must be noted that it is the velocity of water current in contact with the oysters and not that at the surface of the bays that is of importance. Conclusions based only on measurements of velocity of currents at the surface of the bays would not be reliable.

8. The role of self-silting as a factor in oyster mortality becomes of increased potential importance in bays where velocity of bottom water flow is limited or where water is more or less quiescent, and therefore subject to rapid local rise of temperature during seasons when the respiratory reserve of glycogen for partial anaerobic respiration is at a low level.

9. The self-silt deposit of the oyster is more stable and resistant to flow traction than some materials deposited by gravity.

10. Even if the self-silt is removed from oyster beds by bottom water currents, the self-silting process would increase the effectiveness of the ordinary sedimentary process by gravity.

11. In parts of an oyster reef where active growth occurs, water currents must be sufficiently strong to compensate for silting effects.

LITERATURE CITED

Lund, E. J. 1957. A quantitative study of clearance of a turbid medium and feeding by the oyster. Publ. Inst. Mar. Sci. Univ. Texas, 4(2): 296–312.

Effect of Bleedwater, "Soluble Fraction" and Crude Oil on the Oyster[1]

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Introduction

The problem of estimating effects of wastes from the oil industry on oysters with which we are concerned lies entirely within the field of practical or applied physiology. The whole problem may be approached by determining (a) the time and concentration thresholds of direct effects of these substances on the oyster and (b) whether or not the direct effects of these substances may have indirect effects on the oyster by modifying or removing factors. For example, the effects of the wastes on the food supply in the environment, upon which the continued life of the oyster depends, must be studied.

If no effects of bleedwater, "soluble fraction" and crude oil in these two respects occur then no pollution problems for oyster culture exist so far as presence of these substances are concerned. If reliable answers to the problems under (a) and (b) are to be obtained from experiments, they must be kept separate in the conduct of experiments. In this paper we shall limit the experimental inquiry to the first part of the problem.

SELECTION OF CRITERIA FOR THE DETERMINATION OF THRESHOLDS OF EFFECT OF BLEEDWATER, "SOLUBLE FRACTION" AND CRUDE OIL OF THE OYSTER

The most suitable physiological indices which are available for determining effects of these substances in the oyster are: (a) Death, that is, measurement of survival time; (b)

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[1] This investigation was supported by funds from the Texas A&M Research Foundation. Editor's note: This manuscript was submitted in 1950 as part of Project 9 of the Texas A&M Research Foundation on work carried out at the Institute of Marine Science and is published in essentially original form.

Rate of growth; (c) Shell closure and opening which depend upon neuromuscular mechanisms; (d) The rate of propulsion of the water stream through the gills, and finally; (e) An index which has not hitherto been used by investigators viz., the rate of clearance of turbid sea water.

In studying the effects of any chemical substance or physical agent on any of these indices it is important to remember the general fact that the effect of any agent involves the inverse relation of two factors, (1) concentration of the chemical, *e.g.* bleedwater, and, (2) the duration of application of the agent. Since in general the (time) x (concentration) principle is applicable, then effects under field conditions involving a long time and very low concentrations of the agent may have effects which would not be detected in experiments of short duration. For this reason the slow process of growth (index b) or the long but finite time of survival (index a), are more suitable as practical indices in the field than in laboratory experiments. From these facts it follows that unless the time and concentration factors of bleedwater and oil in laboratory experiments are comparable to those in the field on the oyster bed then it is not permissible to apply the results and conclusions from laboratory experiments to field conditions and vice versa. Failure to comply with this requirement in drawing conclusions was the error made by Galtsoff (1935) when he erroneously applied conclusions from laboratory experiments on effects of bleedwater, "soluble fraction" and oil on the oyster to field conditions.

Furthermore, since the concentrations of bleedwater, crude oil and the so called "soluble fraction" occurring in the field are extremely low, and hence the duration factor must of necessity be large for observable effects to occur, then the indices of survival, and growth are only of practical significance when used in field experiments of long duration, since field conditions of long duration cannot be duplicated in the laboratory. This is where the experiments by Hopkins, Mackin and Menzel on growth and mortality in the field are properly applicable to the problem (Hopkins, Mackin, and Menzel, 1954; Menzel and Hopkins, 1955).

The propulsion of water through the gills has been extensively used as a physiological criterion for response of the oyster to external agents (Galtsoff *et al.*, 1935; Loosanoff and Engle, 1947; Collier and Ray, 1948). Although the rate of flow of sea water through the oyster is a very useful and important index of function, it is unfortunate that some investigators have erroneously assumed that the volume flow through the oyster is a *measure* of its *feeding* activity. That such a relation exists has never been shown. The feeding process may stop entirely while the flow of water continues Lund (1957)).

CLEARANCE OF TURBID SEA WATER AS AN INDEX

The advantage of using the rate of clearance of a sea water suspension is that its rate may be accurately followed. Furthermore, the volumes of materials removed from the sea water and the volumes of feces and rejecta produced may also be independently and simultaneously measured. Another advantage of the clearance index is that the oyster is not placed in constraint as may readily occur when volume of water flow is measured by other methods. Furthermore, many oysters may be used simultaneously in the same clearance experiment instead of only one as in pumping experiments. For simplicity the first experiments on the effects of bleedwater, oil and "soluble fraction" on clearance will be shown without simultaneous measurement of the volumes of the feces and rejecta. The conditions of the following experiments are further restricted by observing clearance in a fixed volume of medium in glass aquaria.

Experimental Studies

THRESHOLD CONCENTRATION OF BLEEDWATER AFFECTING CLEARANCE

EXPERIMENT OF FEBRUARY 14, 1949

Since clearance of a suspension of sea water depends upon the action of surface cilia, we should expect clearance to be a very sensitive and reliable index of the effects of bleedwater and oil, since such substances come first into contact and have their effect on the external ciliated surfaces of the oyster.

The sample of bleedwater used was a composite from different wells, Number OW-2a-Pk-J having a salinity of 120.4‰. The sea water used as a diluant had a salinity of 28.3‰. Thirteen large glass aquaria each containing 14 liters were arranged in two lots.

The 6 aquaria in one lot contained 0.0%, 3%, 6%, 9%, 12% and 15% bleedwater by volume in sea water. These were set aside as controls for determining the rate of clearance due to the precipitating effect of ions in sea water and deposition by gravity as in a preceding paper (Lund, 1957a).

The rate of clearance by gravity in each one of these aquaria is given in the dotted curves of Figure 1. Since the bleedwater was itself quite turbid, it will be seen that addition of increasing volumes of bleedwater decreased the initial light transmission of the sea water used as the diluant. Note also that the higher the concentration of bleedwater the more rapid is the clearance by gravity. The blank, B1, with sea water alone shows the slowest rate of clearance as indicated by the slope of its curve.

To each aquarium of a duplicate set of 6 aquaria with the same concentrations of bleedwater, were added 10 oysters. These were one year old oysters all grown from spat under known conditions. They were carefully cleaned and free from external parasites. It will be seen that beginning at corresponding turbidities each lot of these oysters cleared the 14 liters of bleedwater-sea water mixtures to 95%–100% transmission in 24 hours. Clearance was completed first in pure sea water of lowest turbidity; clearance of the mixtures of higher turbidity followed. After completion of the test the oysters were removed to pure sea water for prolonged observation. There was no mortality among the 60 oysters used until March 12, 1949, about a month after the experiment, when only one died.

It is evident that the clearance in an aquarium containing oysters is the result of both the clearance effects by the oysters and precipitation by ions of the sea water. Theoretically, correction for the ion effect could be made by subtracting the curves of ion effect from the corresponding curves of clearance in the aquaria containing oysters. However, the fact that the presence of oysters causes some turbulence, not present in blanks without oysters, makes such correction of less significance. The important fact shown by the experiment is that the oyster is able to clear even a 15% concentration of bleedwater in pure sea water, without evidence of permanent injury.

A 3% mixture of bleedwater (120.4‰) and sea water (28.3‰) has a salinity of 31.06‰. If a 3% mixture produces a threshold effect because of salinity one concludes that the change of salinity from 28.3‰ to 31.06‰ is the minimal change required.

Since clearance may be taken as a reliable and very sensitive index of normal stimulation, it becomes evident that bleedwater encountered in the field in concentrations below 3% would be entirely without effect on the normal sensitive clearance function of the oyster.

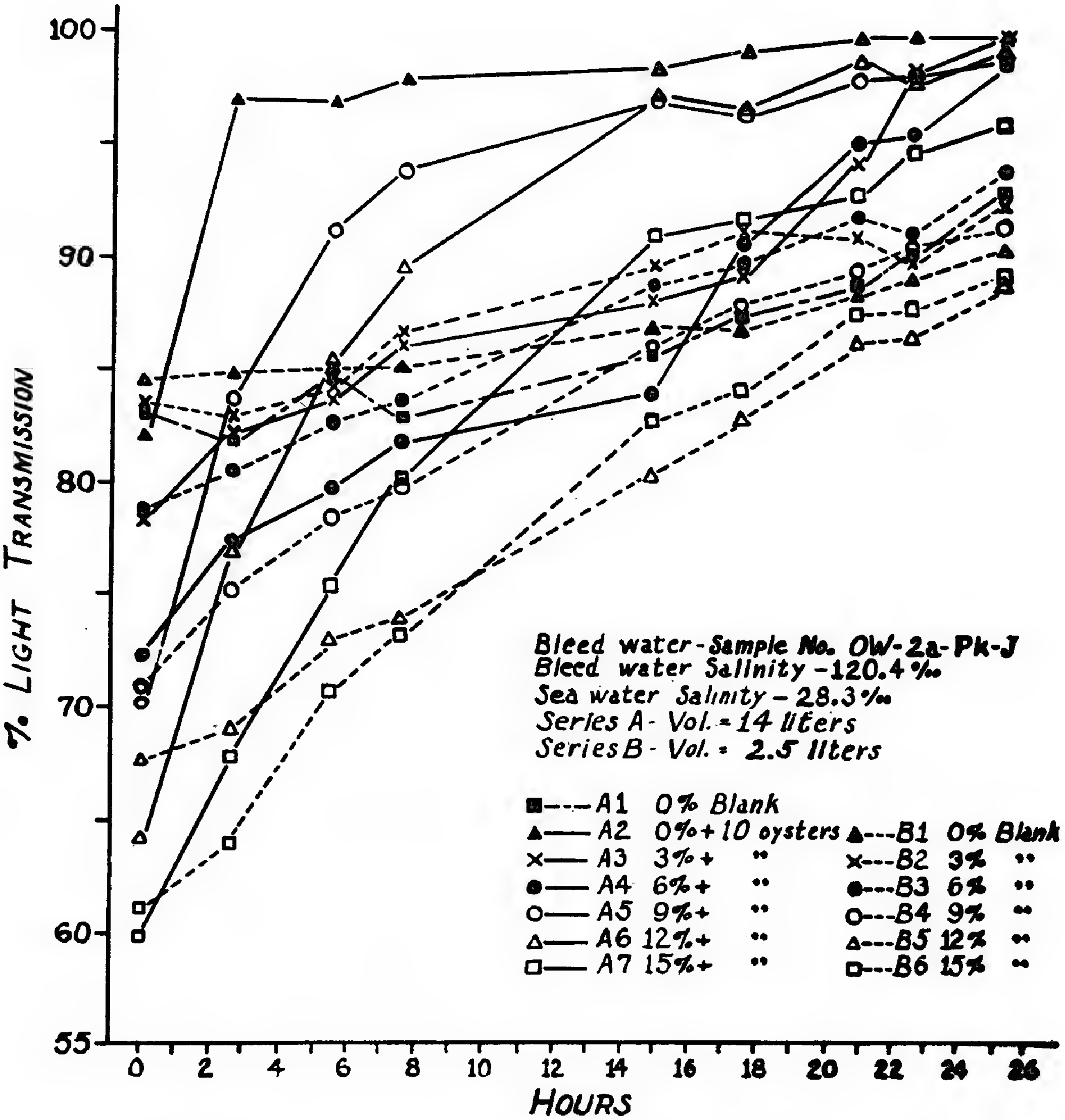

Fig. 1. Effect of varying concentrations of bleedwater on the rate of clearance of turbidity by oysters. Control tanks do not contain oysters. Per cent transmission is shown increasing with time.

It must be emphasized as shown above that this is a stimulus response threshold and is many times below any injury threshold concentration since exposure of the oyster for a period of 22 hours to 15% bleedwater showed no injury effects.

EXPERIMENT OF FEBRUARY 16, 1949

The essential procedure in the previous experiment was repeated on a new lot of 60 oysters grown from spat under continual observation.

These oysters were free from all external parasites. The only change in procedure was the reduction of the volumes of the solutions in the aquaria. In this way the time for clearance by the oysters was reduced to less than 15 hours. The curves in Figure 2 show the results. It will be observed that the decreasing order of average rates of clearance is now 0%, 3%, 6%, 9%, 12% and 15% bleedwater.

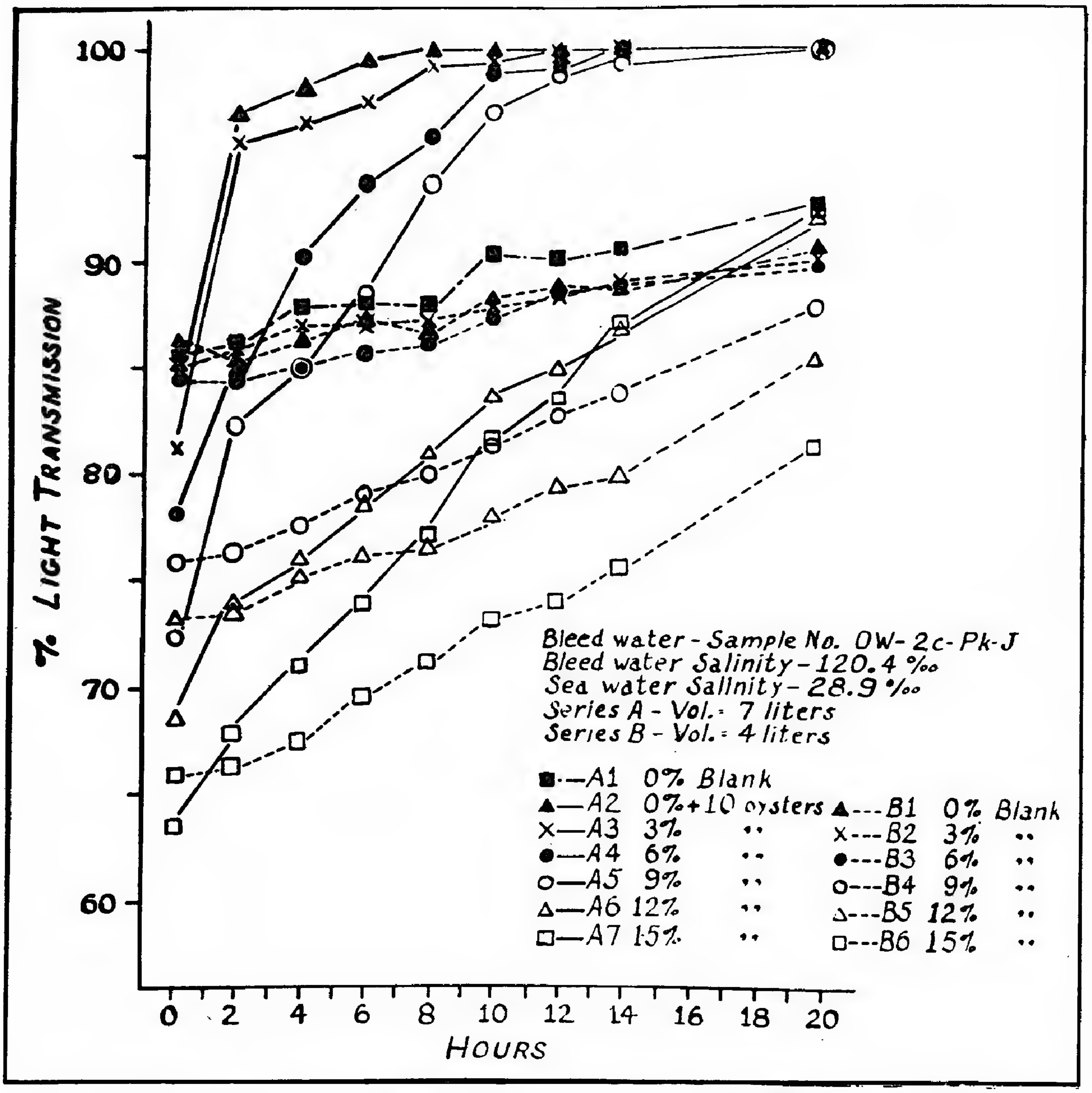

FIG. 2. Effect of different concentrations of bleedwater on speed of filtration by oysters in enclosed tanks. Control tanks do not contain oysters.

The ten oysters in each of the concentrations 0.0%, 3%, 6% and 9% bleedwater all completed clearance of seven liters in approximately 12 hours, while those in 12% and 15% showed only a 90% completion of clearance at the end of 19 hours. It is evident that a concentration of 3% bleedwater may be considered as a threshold value, *i.e.*, having a threshold effect on the ciliary mechanisms.

The same sequence in effects of concentrations of ions on the precipitation by gravity is shown in this and the previous experiment. Note that the two duplicate blanks A1 and B1 closely parallel one another in rate of self clearance in pure sea water. All of the 60 oysters used in this experiment were living and active on March 8, 1949, more than three weeks later.

Repetition of these experiments yielded the same type of results.

We may therefore conclude that healthy oysters under the above conditions of experiment were able to clear concentrations of bleedwater of 120‰ salinity in sea water of 28‰ salinity, up to at least 15%, the threshold concentration for minimal effect of this bleedwater being above 3%. The 15% concentration of bleedwater in this experiment had a salinity of 41.05‰ and the 3% concentration 31.06‰.

In no case was there any evidence of permanent injury or death to the oysters in these experiments, even in 15% concentrations of bleedwater.

EFFECT OF FULLER'S EARTH ON THE RATES OF CLEARANCE IN MIXTURES OF UNFILTERED AND FILTERED BLEEDWATER

In order to test the ability of oysters to clear bleedwater mixtures when the turbidity was greatly increased by adding fuller's earth suspension, the following experiment was performed. A new lot of 60 "homegrown" clean oysters was used. The volumes of all solutions were 7 liters. The experiment was divided into two parts, (a) using clear bleedwater which had been filtered through a column of cotton and (b) using unfiltered bleedwater (considerable turbidity).

To each of three aquaria containing respectively 3%, 9% and 15% bleedwater which had been filtered, were added 10 oysters. A duplicate set of blanks were also set up as controls, Figure 3.

The second set was similarly made up with unfiltered bleedwater. Two controls of pure sea water were also provided, one containing 10 oysters, the other a blank of sea water. All of the 14 aquaria were allowed to clear for a beginning period of 3½ hours. At the end of 3½ hours 50 cc. of a concentrated fuller's earth suspension was added to each of the 14 aquaria in order to increase the turbidity by equal amounts in each of the aquaria. Note that the oysters in one part of the experiment were allowed to operate on turbidities of both the bleedwater and the fuller's earth suspension. In the other part of the experiment the duplicate lot of oysters only operated to clear the added fuller's earth.

It will be observed from the first part of the curves in Figure 3 that adding the fuller's earth decreased the light transmission in all of the 14 aquaria. However, the oysters in *both* sets, except those in 15% unfiltered and 15% filtered bleedwater, completely cleared the suspensions in less than 8 hours. It took about 20 hours for the oysters in the 15% bleedwater concentration to clear to 97%.

The experiment was now repeated by simply adding a second volume of 50 cc. of the concentrated suspension of fuller's earth at the end of 22 hours. See Figure 3. The repetition of clearance in all the aquaria was again followed by determining the transmission with the Fisher Electrophotometer. The curves show that the oysters again had nearly cleared the suspensions at the end of 32 hours. The increase in slope of the clearance curves in the aquaria without oysters is due to the fact that the fuller's earth suspension is more readily precipitated by ions than materials of the suspension causing the turbidity in the bleedwater. The experiment shows that the threshold concentration for any observable effect on clearance lies above 3% bleedwater, 9% bleedwater being cleared almost as rapidly as the 3% concentration.

All these oysters were living and active for many days after the experiment.

CLEARANCE BY THE OYSTER IN THE PRESENCE OF SO-CALLED "SOLUBLE FRACTION" DISSOLVED IN SEA WATER

I am indebted to Dr. C. K. Hancock of the Department of Chemistry of the A.&M. College of Texas for the preparation of approximately 17 liters of "soluble fraction." It was obtained by counter current extraction of Lafitte "clean" petroleum (No Io-23-

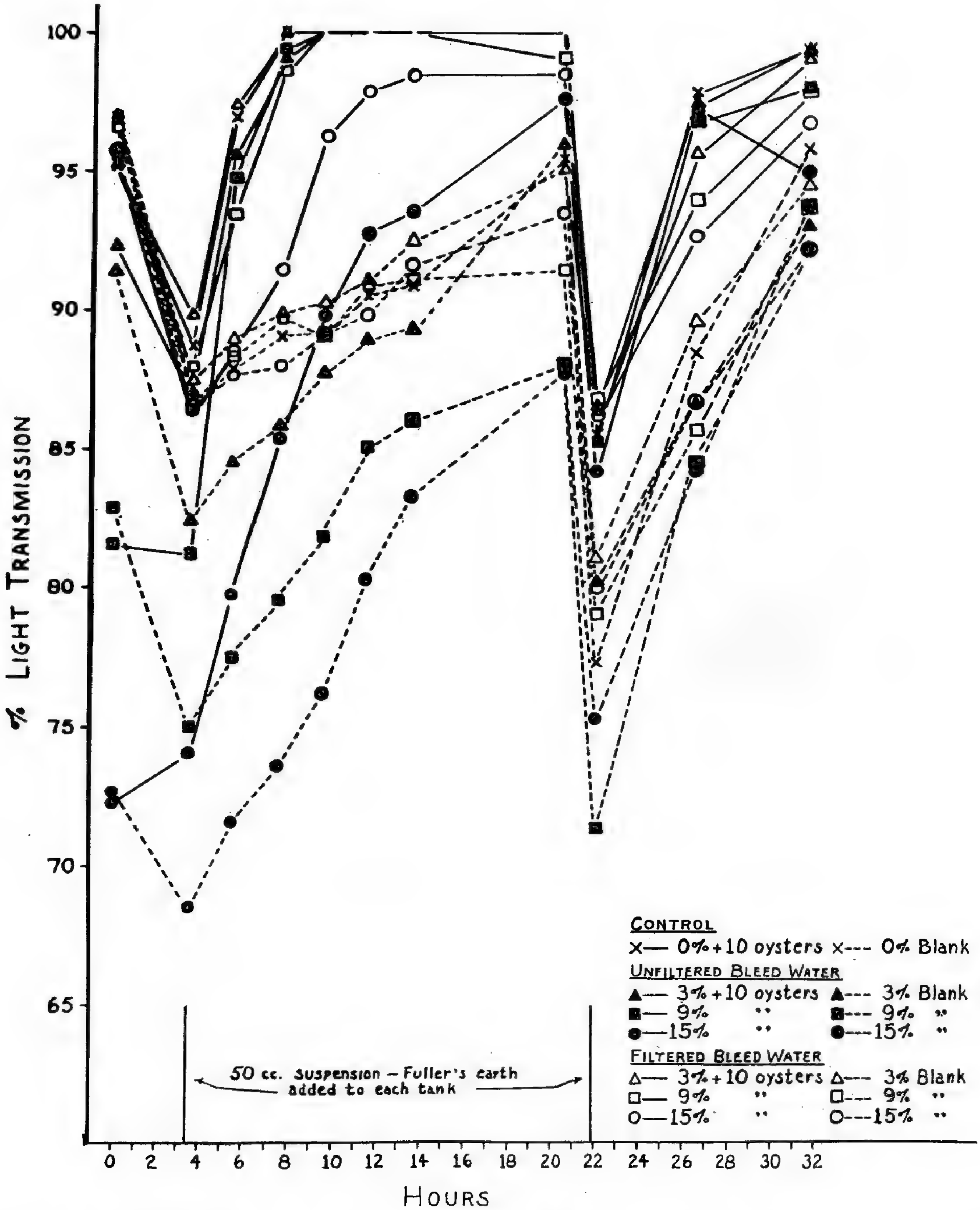

FIG. 3. Rates of clearance by oysters in tanks containing added Fullers Earth. Control tanks do not include oysters.

Kd-J) with Barataria bay water (No AuW-11-Pk-Hk).[2] After extraction the "soluble fraction" mixture had a salinity of 16.01‰. Several tests were made, only one being reported since all showed that no effect on clearance occurred in as high as 6% concentrations of the extract in sea water.

The experiment was set up in the same manner as described above for bleedwater. Volumes of solution each of 14 liters were used. Two sets of 5 aquaria each were set up.

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[2] Designations are of no significance except as a record for Project 9 of the Texas A&M Research Foundation.

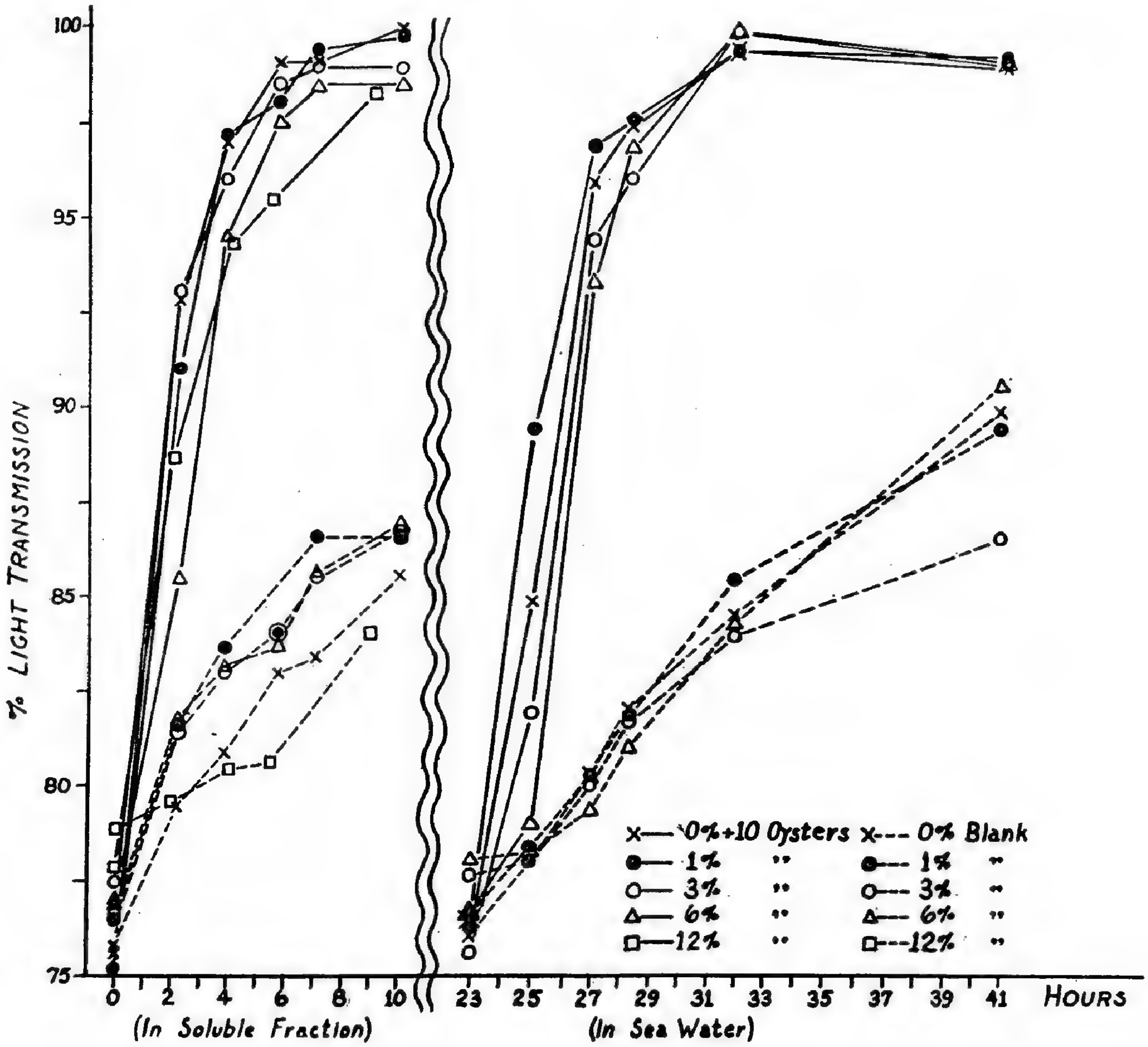


FIG. 4. Effects of different concentrations of "soluble fraction" on the clearance rates of oysters. Control tanks do not include oysters. The graphs on the left indicate rate of clearance in tanks containing "soluble fraction". The graphs on the right indicate rate of clearance of the same oysters after removal from contact with "soluble fraction".

To each aquarium of one set was added ten oysters, while the other duplicate set contained no oysters. The concentrations of "soluble fraction" extract in sea water were 0.0%, 1%, 3%, 6% and 12%. The naturaly turbid sea water of the Pass was used for diluant of the extract and observation of clearance. Since the salinity of the extract was 16.01‰ and that of the turbid sea water was 29.78‰ the addition of the extract in the 12% concentration did not decrease the salinity by more than a maximum of 2‰. Such a change has been shown in other experiments to be entirely negligible.

The first set of curves of clearance in Figure 4 show that within the limits of error there is no detecable effect of the concentrations of "soluble fraction". The rate of clearance by each lot of 10 oysters was practically the same in all aquaria.

In order to see if any residual effect of the extracts on the oysters would develop after exposure of the oysters to the extract, the experiment was repeated except that 14 liters of pure naturally turbid sea water was used for clearance by the same lots of oysters. The curves on the right hand side of Figure 4 show the rates of clearance. All the five lots of 10 oysters each acted normally and showed no after effects due to previous exposure to the "soluble fraction" mixtures. The broken curves show the clearance by ion and gravity effect.

EFFECTS OF BLEEDWATER AND "SOLUBLE FRACTION" ON PUMPING OF WATER BY THE OYSTER

The purpose of the experiments was to determine the effect, if any, of 2.5%, and 5% concentrations of the "soluble fraction" and also to determine whether or not an effect on rate of pumping of water by the oyster could be detected in a 10% concentration of bleedwater in sea water. These were experiments designed merely to approximately check the observations of Galtsoff (1935) made with these substances in these particular concentrations. Galtsoff's (1935) drop method was used but with the addition of an automatic electric counter to record the number of drops of sea water which passed through the oyster. Another simplification was made by our assistant Mr. Ernest Powell, in that he used a toy balloon instead of the rubber apron of Moore (1908) and Nelson (1936), and rubber sheet by other workers, Galtsoff (1935) Loosanoff and Engle (1947) Collier (1948). A rubber toy balloon of suitable size may be cut off to fit any size oyster. After cementing in the usual way the opening of the balloon may be used to connect with the outlet. The experimental arrangement designed by Mr. Ernest Powell is shown in Lund and Powell (1957).

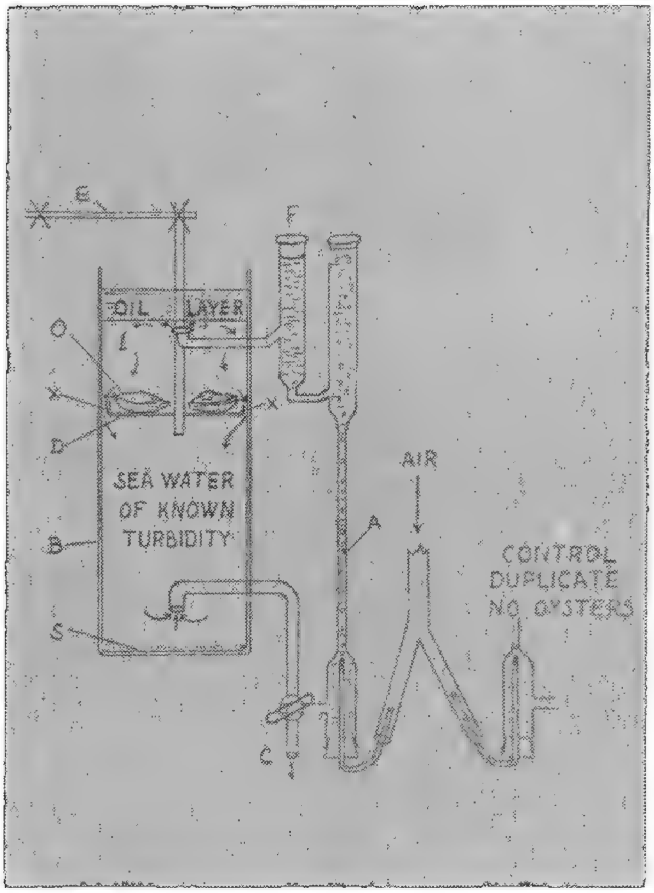
Two kinds of preparation of the oyster were tried: (a) The normal oyster was used with valves free. (b) A section of the right valve was sawed away without injury to the mantle, (A. E. Hopkins, 1935) and a hole was drilled between the valves opposite the excurrent chamber. The two valves were closed by means of a strong rubber band and the excurrent opening was connected to a rubber tube as shown in the figure in Lund and Powell (1957).

It was an interesting fact that the latter preparation seemed to be the most dependable, regular and predictable in its behaviour. It could be left in the open aquarium and used repeatedly. The observed rate of flow varied in our specimens from about 80 to 180 drops per minute but was relatively constant over periods of about an hour. No slowing down or inhibition of the drop rate could be detected when 2.5% or 5% soluble fraction in sea water was applied to the preparation, neither was any significant effect in our preparations observable when 10% bleedwater was used. This latter result corresponds to the observation of Galtsoff (1935).

The primary interest and objective in these experiments was to verify the observations of Galtsoff on the threshold limits of the effects, especially of bleedwater. These threshold concentrations are of practical importance in determining whether or not conclusions from specific laboratory tests are transferable to observed field conditions in respect to concentrations of bleedwater which actually occur in the field.

EFFECT OF CRUDE OIL ON RATE OF CLEARANCE OF SEA WATER

To detect the possible effect of crude oil on the behaviour of the oyster an apparatus was constructed as shown in Figure 5. A cylindrical vessel B, 15 cm. in diameter x 30 cm. high with a capacity of 7 liters, was filled with the turbid sea water. From four to six oysters were placed on a glass stender dish D which fitted loosely into the jar. The stender dish was supported by a glass rod as shown in E. The inlet and outlet of an airlift A were fitted into the vessel B through holes drilled through its wall.



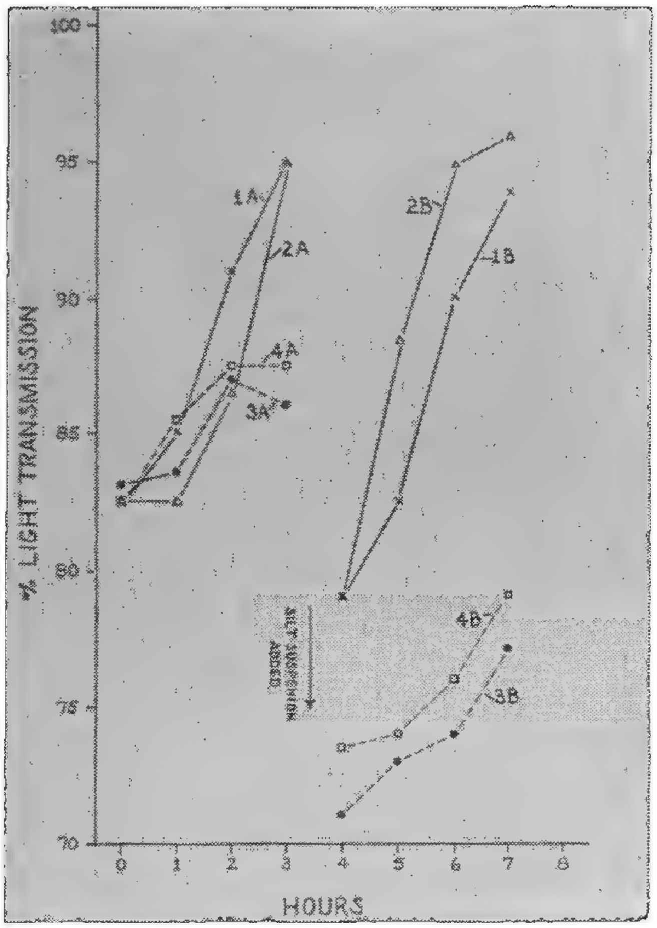


FIG. 5. Apparatus used to study the effect of a layer of crude oil on oyster filtration.

FIG. 6. Effect of a surface layer of crude oil on filtering rate of oysters. Curves 1A and 2A, clearance without oil; curves 2A and 2B clearance under oil; curves 3A and 4A, without oysters.

As the rapid stream of sea water circulated, it continually washed the lower surface of the oil layer (100 cc.). The air lift also maintained adequate aeration for the oysters. By means of this arrangement a copious but non-turbulent circulation of aerated sea water was provided without permitting a mixture of the castings and rejecta to enter the circulation of turbid sea water, since the castings and rejecta settled to the bottom of the supporting perti dish. Precipitation by gravity from the turbid sea water occurred on the bottom of the vessel at S thus partly separating the deposits produced by the oyster from that by gravity.

At regular intervals 60 cc. samples of sea water were withdrawn at C for determination of per cent transmission. After the test the sample was returned to the system at F. A duplicate control apparatus without oil was set up as shown in Figure 5. In this way two curves of the rates of clearance were obtained (Figure 6). As a further control two additional jars of the same capacity were set up without oysters; one of the jars had an oil layer, the other had no oil. The rates of self clearance by ion precipitation were determined in each of these two vessels. The rates of clearance in these blanks are shown in Figure 6, Curves 3A and 4A.

The curves of rates of clearance in the aerated jars containing oysters are shown in curves 1A and 2A. It will be noted that a clearance to 95% occurred in three hours. Since different lots of oysters were used in this experiment it was not to be expected that the curves of clearance should coincide. However, there is no evidence that clearance is inhibited by sea water extracts from the oil layer.

In this experiment a second attempt was made to detect if possible any difference in clearance by these same oysters in the presence and absence of oil by adding 25 cc. of a heavy natural silt suspension. The silt used was that collected from sea water which had been self cleared by ion precipitation.

It will be observed that adding the silt suspension to each of the vessels containing the oysters lowered the transmission to about 78% while in the blanks this was reduced to between 71% and 75% due to restirring of the sea water.

Curves 1B and 2B show the rates of clearance by the oysters in contact with oil. The clearance shown in curve 2B was if anything more rapid than that by the oysters in the absence of oil, Curve 1B.

The experiment clearly shows that in such a *closed* system if any marked inhibitory effect of oil extracts on clearance did exist they would have ben detected. Several other experiments of this type which are not presented also gave negative results.

Finally, we attempted to determine if any effects of oil (extracts) could be detected when measurement was made of the total volumes of castings and rejecta formed in the presence and absence of oil.

EFFECT OF CRUDE OIL ON THE RATES OF FORMATION OF CASTINGS AND REJECTA BY OYSTERS IN TURBID SEA WATER

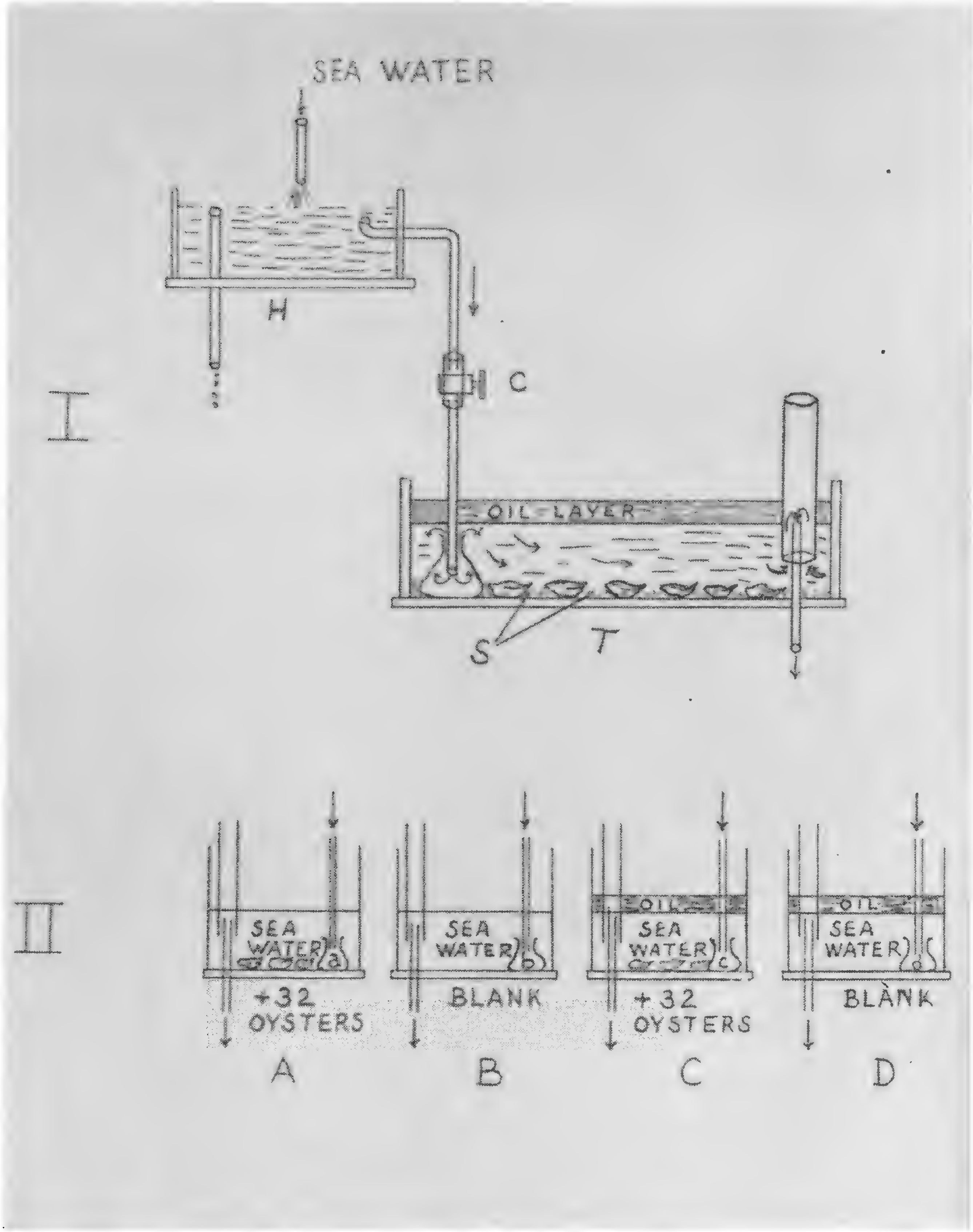
In the opinion of the writer probably the most sensitive and crucial test to determine if oil extracts affect the clearance function of the oyster is shown by the following procedure.

A constant level sea water supply aquarium holding 50 liters was suspended as shown in Figure 7. I,H. It was supplied by a large stream of sea water pumped directly from the Pass. Thus the sea water supply was practically at the same temperature, turbidity, salinity and food content as that in the Pass.

Four identical fifty liter aquaria were set up as shown in Figure 7 II, A, B. C. and D. Each of these aquaria was supplied by a constant stream of sea water from the common head supply tank H. The rates of flow in all the four aquaria were regulated and made equal by screw pinch cocks C. On the bottom in each of aquaria A and C were placed 32 selected oysters. These oysters came from a lot of 400 carefully selected Louisiana oysters shipped from Barataria bay. They had been grown from spat and were approximately 18 months old and measured about 1½ to 2½ inches in length. Before using them in experiments they were acclimated for six days to the higher salinity (27‰) of the sea water at the Port Aransas Laboratory. Aquaria B and D contained no oysters. One liter of crude oil (FO-lf-Kd-J) was placed on top of the sea water in each of aquaria C and D. The depth of the sea water layer in all aquaria was 10 cm. Flasks of 125 cc. capacity a, b, c, d were placed under each intake and used as a trap for coarse sediment. However, practically all coarse sediments were caught in the common supply tank H. Turbidities at the inlet and outlet of each aquarium were determined every 12 hours.

At the intake and outlet in aquaria A and C there was always a marked difference in turbidity due of course to clearance by the oysters. The corresponding differences in B and D were always small. It will be observed that this experiment, as compared with the preceding one, represents the oyster operating in an *open system* under more nearly natural conditions of change of sea water, availability of food, temperature, salinity, and turbidity, and during a relatively long period of eleven days.

At the end of eleven days the oysters were removed for future observation. The accumulated silt deposits in each aquarium were carefully collected into four 1000 cc. cyl-


SEA WATER
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OIL
SEA WATER
c
+32 OYSTERS
C
OIL
SEA WATER
d
BLANK
D

FIG. 7. Aquaria used in experiments on the effect of oil on oysters.

inders, left to settle for 5 hours after which a photograph was taken to show the volumes of solids. A photograph of similar type is Figure 3 in Lund (1957b). The ciliary clearance mechanism in the 32 oysters exposed to the oil layer had operated equally well or slightly better than that in the duplicate control lot A without contact with oil. Similar amounts of silt had accumulated. One oyster in aquarium B (no oil) had died. All the other 63 oysters were alive at the end of the experiment of 11 days duration. One other experiment similar to the one just described but lasting five days also showed no effect of oil under the conditions of the experiment.

The general conclusion is, therefore, that no detectable effect of crude oil on the sensitive clearance function of the oyster can be demonstrated when the rate of clearance of the medium and volume of self-silt accumulated are used as indices.

Attention should be called to the original experiments by Prytherch (pp. 160–162 in Galtsoff, 1935) which showed that intermittent *immersion* in crude oil did not kill the oysters he used. Death or injury of an oyster due to oil, when used as a criterion (cf. above), is an exceedingly crude index and involves drastic procedure compared to the reversible and highly sensitive test of clearance of turbid sea water by the oyster.

Summary

(1). The capacity of an oyster to clear turbid sea water suspensions has been used as a physiological index. Clearance of turbid sea water was used to determine effects of crude oil, bleedwater, so-called 'soluble fraction,' and their theshold concentrations as stimuli.

(2). The sensitivity threshold of a concentration of bleedwater having a salinity of 120.4‰ when diluted with sea water at 28.3‰ is above 3% concentration of bleedwater The range of threshold concentrations for effect on clearance lies between 3%–6% of these bleedwater mixtures.

(3). The clearance of a turbid suspension in sea water is a more sensitive physiological index than propulsion of water, since bleedwater in a 3%–6% concentration only is required for an effect on clearance while a 10% concentration or more is required for threshold effect on water propulsion.

(4). Ten oysters can clear 14 liters of concentrations of this bleedwater up to 15% without any evidence of permanent or temporary injury to the oysters.

(5). Increasing the turbidity by increasing the concentration of the suspension with fuller's earth in the bleedwater mixtures did not affect the capacity of the oyster to clear such suspensions.

(6). The so-called "soluble fraction" obtained by counter current extraction of crude Lafitte "clean" petroleum (Number Io-23-Kd-J) with Barataria Bay water had no effect on clearance or water propulsion by the oyster in 6% concentration in sea water.

(7). Two methods were devised for testing effects of crude oil on the oyster. The first method involved circulation of a 7 liter volume of aerated turbid sea water in contact with crude oil, in a closed system containing oysters. No effect on the rate of clearance by the oysters could be detected.

The second method was that of testing the effect of a constant stream of sea water in continuous contact with crude oil on the rate of feeding and rejection of the natural suspension including plankton in sea water. The experiments showed that the crude oil had no effect on the volume of suspended matter (food plus inert material) taken in by the oyster over a period of eleven days. This procedure is thought to be the most sensitive test yet devised for determining the effect of crude oil on the ciliary mechanism of the oyster.

LITERATURE CITED

Collier, A., and S. M. Ray. 1948. An automatic proportioning apparatus for experimental study of the effects of chemical solutions on aquatic animals. Science, 107: 576–577.

Galtsoff, P. S., ————. 1935. Effects of crude oil pollution on oysters in Louisiana waters. Bull. U.S. Bur. Fish., 48: 142–210.

Hopkins, A. E. 1935. Temperature optima in the feeding mechanism of the oyster, *Ostrea gigas*. J. Exper. Zool., 71: 195–208.

Hopkins, S. H., J. G. Mackin, and R. W. Menzel. 1954. The annual cycle of reproduction, growth, and fattening in Louisiana oysters. National Shellfisheries Assoc. Convention Papers, 1953: 39–50.

Loosanoff, V. L., and James B. Engle. 1947. Effect of different concentrations of micro-organisms on the feeding of oysters *(O. virginica)*. U.S. Fishery Bull. 42; Bull. U.S. Fish and Wildlife Serv., 51: 31–57.

Lund, E. J. 1957a. A quantitative study of clearance of a turbid medium and feeding of the oyster. Pub. Inst. Mar. Sci. Univ. Texas, 4(2): 296–312.

————. 1957b. Self silting by the oyster and its significance for sedimentation geology. Pub. Inst. Mar. Sci. Univ. Texas, 4(2): 320–327.

Lund, E. J., and E. Powell. 1957. Note on the reflex inhibition of water propulsion by the oyster. Pub. Inst. Mar. Sci. Univ. Texas, 4(2): ....

Menzel, R. W., and S. H. Hopkins. 1955. The growth of oysters parasitized by the fungus *Dermocystidium marinum* and by the trematode *Bucephalus cuculus*. J. Parasit., 41: 333–342.

Moore, H. G. 1908. Volumetric studies of the food and feeding of oysters. Bull. U.S. Bur. Fish., 28: 1295–1308.

Nelson, T. C. 1936. Water filtration by the oyster and a new hormone effect upon the rate of flow. Proc. Soc. Exp. Biol. Med., 34: 189–190.